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The Life-History of Nucula delphinodonta (Mighels)

BY

GILMAN ARTHUR DREW

Professor of Biology

ORONO, MAINE
November, 1901

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THE LIFE-HISTORY OF NUCULA DELPHINODONTA (MIGHELS).

The material upon which these observations were made was secured at Casco Bay, Maine, during the summers of 1897 and 1898. Nucula delphinodonta is a small form, seldom growing to be more than 4 mm. in length, and as it lives below low-tide mark it is not very well known by collectors. By using a sufficiently fine dredge, however, unlimited numbers of adult and young specimens may be procured. Individuals may be found living under very different conditions; in inlets and protected places, and exposed to the open sea, and from near low-tide mark to a depth of several fathoms. The principal habitat, however, is in the shallow inlets and near the heads of sounds, where the bottom is composed of fine mud, mixed with some sand, broken shells, and decaying vegetable matter. Individuals are most numerous just outside of the eel grass which skirts the shore where the bottom is of this character, in water which at low tide is from one to three fathoms deep. The mud in which they live is much like that inhabited by Yoldia limatula, except that it is not so free from shore débris. Although some specimens may be obtained where Yoldia is most abundant, they are generally more numerous somewhat nearer the shore, and they may be very numerous at considerable distances from places where Yoldia is known to thrive.

In picturing the conditions under which these animals live along the coast of Maine, the reader should not fail to take into account the average tide of about ten feet, which keeps the water very pure over a comparatively foul bottom. The fauna and flora of these bottoms are very abundant and diversified, but have not been carefully catalogued. Diatoms of several species abound, and form a large part of the food of Nucula. Other Algæ, Ostracods, Foraminifers, small Lamellibranchs, and Gastropods are also very abundant, and small individuals of most of these forms are occasionally found in the stomachs of preserved specimens.

While I have never succeeded in getting individuals to form brood-sacs in captivity, they live well in aquaria, and may be kept for several weeks either in vessels containing the mud in which they normally live, or in vessels without this mud. It is not even essential that the water be changed very frequently.

When placed in vessels containing mud they bury themselves, and seem never to come to the surface to stay for any considerable time. They are at all times comparatively sluggish, and seem to wander around in the mud by slow thrusts and retractions of the foot, which is a very perfect burrowing organ. When placed in mud that is just sufficiently deep to cover them, their movements can be followed fairly well by the movements of the mud. To see them feeding it is necessary to use only a very thin layer of mud. The action of the palp appendages can then be observed. They perform the same function that is performed by similar appendages on the palps of Yoldia (1), that is, they are food collectors. Nucula delphinodonta seem normally to feed beneath the surface of the mud, so feeding cannot be observed as easily as it can be in the case of Yoldia (text-fig. T).

The movements of the foot are best observed by placing specimens in shallow dishes of sea water. When specimens are placed on mud they bury themselves so promptly that the movements of the foot cannot be carefully followed. The movements are all such as would be of service in burrowing in mud. Although specimens have been kept under observation under different conditions for long periods of time, I have never known one to execute movements that could be interpreted as creeping. In 1853 Forbes and Hanley, in describing Nucula nucleus (4), made the following statement:—"The foot is white, and as if pedunculated and deeply grooved, so as to expand into a broad leaf-shaped disc with serrated margins; by means of this organ it can creep like a Gasteropod, and we have seen it walk up the sides of a glass of sea water." This seems to be the only observation of this kind on record, although many students have worked on this and related forms. The authors who have adopted the view that the foot functions as a creeping organ in members of this group have, in nearly every case, had only preserved material to work upon, and perhaps have been influenced by finding so many characters that seem to them to denote generalised structure. Some Lamellibranchs are able to pull themselves over smooth surfaces, but my observations lead me to believe that the form and structure of foot found in this group is especially poorly adapted for such a purpose (3). The expanded foot of Nucula delphinodonta is relatively very large, and the almost spherical shell is frequently turned from one side to the other, but nothing comparable to creeping has been observed.

Although many Lamellibranchs carry their eggs and developing embryos, I think this is the first case reported where a special external sac is formed for the purpose. This sac (fig. 1) is composed of a mucus-like material, mixed with foreign bodies, and is attached to the posterior ends of the valves of the shell. Although the process of making the sac has never been observed, it seems probable that the mucus-like material is secreted by the hypobranchial glands. This material is probably passed posteriorly by the action of the cilia on the mantle, and very likely the respiratory currents of water swell it into a sort of bubble that remains attached to the posterior ends of the shell-valves, and, while still soft, adheres to the foreign particles with which it comes in contact.

That the hypobranchial glands are concerned in the formation of the material from which the brood-sac is formed is indicated by their appearance before and after the sacs have been formed. In females in which the ovaries are still full of eggs, the cells of the hypobranchial glands are large and gorged with secretions, while in females that have formed the brood-sacs the cells are shrivelled and almost devoid of secretions.

The eggs are deposited in the brood-sac (fig. 1), and in it the embryos are carried until they reach an advanced stage in development, probably for a period of three or four weeks.

The eggs of this species are brown, opaque, few in number, and correspondingly large. From about twenty to seventy may be found in a sac, and they average about .21 mm. in diameter. Each egg is enclosed in a membrane that is probably secreted by the egg, but its formation has not been observed. Fertilization is probably accomplished in the brood-sac. Eggs and young embryos do not live well after they are removed from the brood-sacs, so the ages of the various stages have not been determined. Processes of maturation and cleavage proceed slowly. The time between the appearance of the first and the second polar body is frequently as much as two hours, and the time between cleavages seems to be nearly or quite as long. It is not beyond doubt, however, that the removal of the eggs from the brood-sacs influenced the length of time. That development is slow is not to be doubted. Embryos taken from the brood-sacs of specimens kept under as nearly natural conditions as possible for a month, had only reached the stage where two gill-lobes were formed.

It seems probable that the polar bodies may be formed by eggs that have not been fertilised. Eggs were sometimes obtained that formed polar bodies and developed no further.[1]

Just before each polar body is formed, a more or less distinct, and frequently a very pronounced swelling, makes its appearance on the side of the egg opposite the point where the polar body will appear. In the preparation for the first cleavage a similar swelling is formed on the side opposite the polar bodies. When the egg divides, the dividing wall passes to one side of this swelling. The two blastomeres are accordingly rather unequal in size. The difference in the size of the two blastomeres seems to depend upon the size of the swelling that precedes their formation. Cleavage into four and eight cells (text-figs. C and D) are typical. The polar bodies retain their position on the animal pole until the embryo acquires cilia, when they are rolled around on the inside of the membrane. No attempt has been made to follow out the fate of the individual cells.

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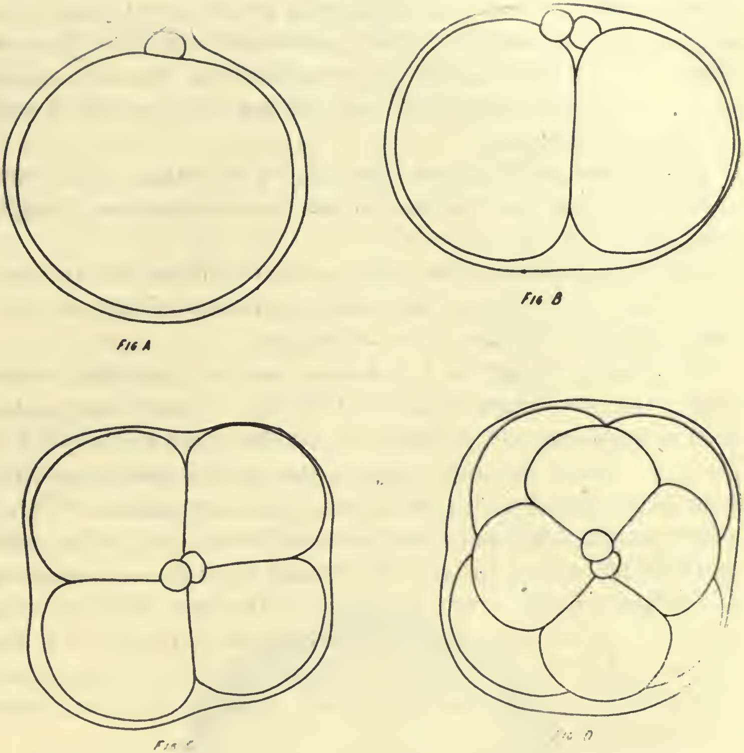
[1] Most of the eggs of an isolated specimen of Nucula proxima, a form that throws its eggs free into the water, formed the polar bodies, and a few eggs cleft the first time. It is possible that some sperm were in the water, but the water had not been changed for nearly twenty-four hours before the eggs were laid, and sperm of this species do not seem to retain their vitality for nearly so long a time.



Text-figs. A, B, C, and D.—Early stages in the development of Nucula delphinodonta.

In the sixteen-celled stage (figs. 2 and 3) a small cleavage cavity is present. Later this becomes slightly more pronounced. The cells on one side of the blastula divide more rapidly than those on the other side, and push over them in the form of a cap (fig. 4). A pocket appears between the large cells at such a point as is indicated by the asterisk in fig. 4. Just how this pocket is formed is still a matter of some doubt, but it seems to be formed by the separation and division of some of the larger cells. This pocket (fig. 8) can now be compared with the invaginate portion of a gastrula. It represents the first appearance of the gut.

About the time that the pocket is formed most of the smaller surface cells acquire cilia (fig. 6), and the embryo begins to roll around in the membrane. The cilia are all short, similar in appearance, and seem to be evenly scattered over the surfaces of the cells. In whole mounts the boundaries of the surface cells are not very distinct, but the cells do not seem to have a very definite arrangement.

From these small surface cells, that at this stage appear very much alike, the test,[1] the apical plate, and the cerebral ganglia are formed.

The large cells near the blastopore do not bear cilia, at least none could be found on preserved specimens. They are concerned in the formation of the shell-gland.

The embryo is still nearly spherical, and so opaque that, while alive, internal changes cannot be followed. A few cells, probably the beginning of the mesoderm, lie above and by the sides of the gut. About this time some of the surface cells around the blastopore divide, and push in to form a stomodæum. Other cells near the blastopore become enclosed by the surface cells, and together with cells probably derived from those forming the stomodæum, finally form a portion of the new ectoderm, that soon covers the body of the embryo inside of the test. When the ectodermal layer is complete it joins, but does not enclose, the stomodæum. In position as well as origin the stomodæum is ectodermal.

Before the ectodermal layer is complete the embryo begins to elongate, and the surface cells close in over the shell-gland from the sides and anterior end. At the same time the surface cells become arranged in rather definite rows. It is very difficult to get satisfactory views of these cells in whole mounts, but there seem to be five rows, beside a group at the anterior end that forms the apical plate. Two or three of the posterior rows are interrupted in the region of the shell-gland, but this interruption disappears as the shell-gland becomes closed in. Closing is never complete. A small opening is left dorsal to the blastopore, separated from it by the width of one test cell (fig. 15). The anus comes to lie near this opening at a later stage (fig. 24). Before the shell-gland is covered, the gut turns toward the dorsal side (fig. 11, *mg.*), and the mesoderm cells take up a position near the posterior end of the embryo. Two of the mesoderm cells are large, and have very large and conspicuous nuclei. These cells are far posterior, and lie side by side.

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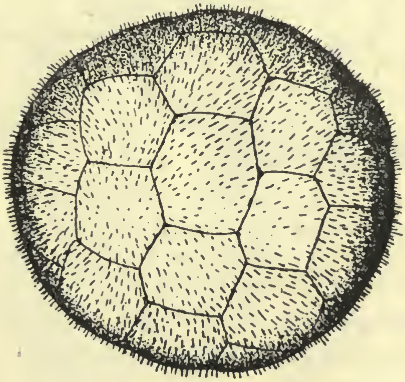
[1] I use the term "test" here, as in former publications, to designate the surface cells that bear cilia and may be homologized with the velum of other forms.

Soon after the shell-gland is covered, the gut begins to grow posteriorly, almost, if not quite, in contact with the shell-gland dorsally, and separated from the stomodæum ventrally by a few mesoderm cells (fig. 15). A small space appears among these mesoderm cells, which later becomes connected with a space that is formed between the gut and the shell-gland.

At no stage in its development is the shell gland invaginated. From the time of its formation it arches dorsally to some extent (figs. 7 and 9, *sg.*). Just before it becomes covered by the test it flattens somewhat (figs. 11 and 12), but it soon arches dorsally again and becomes quite convex (fig. 17, *sg.*).

The cells that give rise to the cerebral ganglia are few in number (fig. 15, *cg.*), and lie ventral to the anterior end of the stomodæum. They frequently come to the surface, but they may be entirely covered by test cells. A more or less distinctly recognisable test cell lies between the cerebral ganglia and the apical plate, but beneath this test cell the the cerebral ganglia and the apical plate are in contact. The two cerebral ganglia seem to

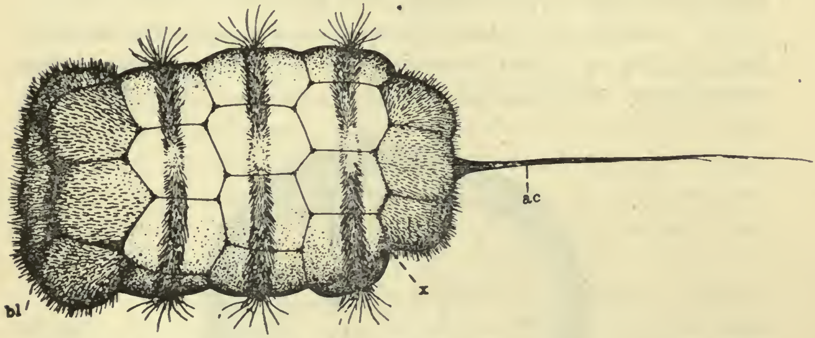


TEXT-FIG. E.—Surface view of a young embryo of Nucula delphinodonta.

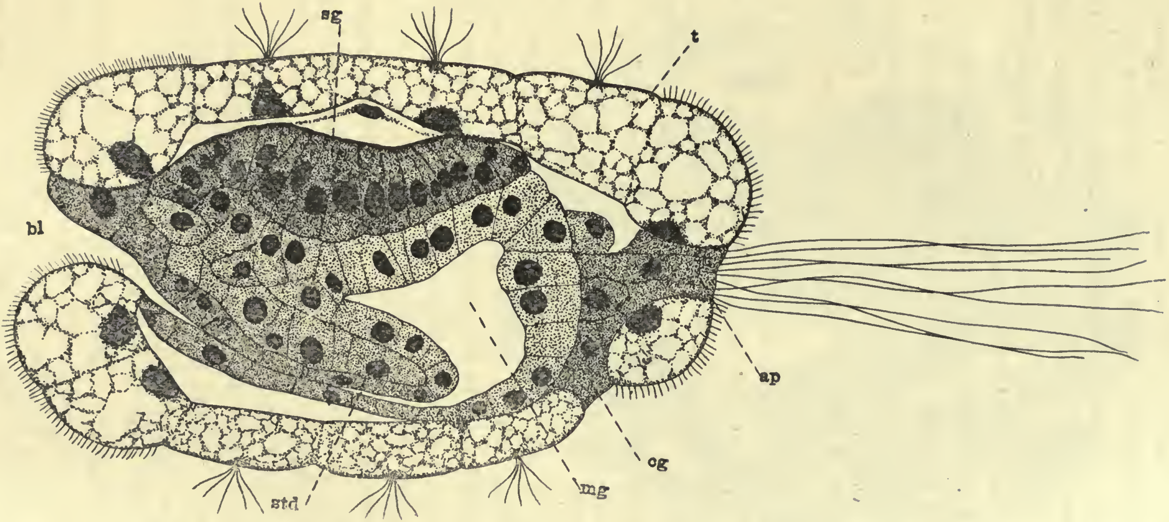
originate from a single mass of cells. There is no indication of the formation of cerebral pouches, as in Yoldia (text-fig. V). The position occupied by the developing body of Nucula does not make it necessary for the cerebral ganglia to shift their position from the point of their formation until the test is shed.

The apical plate is composed of a number of cells, the walls of which are rather indistinct (fig. 15, *ap.*). They bear cilia that in size and distribution resemble those that cover the test cells.

Under favourable conditions the test cells can be seen to be arranged in five rows; occasionally part of a sixth row is present. As in other stages, the boundaries between the test cells are poorly marked, and it is quite impossible to sketch them accurately. Text-fig. E shows their general arrangement, but it must be understood that this is quite diagrammatic. The cilia on the test cells of this species are not collected into bands as they are in Yoldia (text-fig. F), but are evenly scattered over their surfaces. The embryo becomes free from the egg membrane about the time that the shell-gland becomes covered by the test, but the cilia are barely powerful enough to move the embryo slowly on the bottom of a dish. The absence of the bands of cilia, and of the long tuft of apical cilia, is probably due to the protected life of the embryo. Nucula proxima lays its eggs free in the water, where they are fertilised and develop. These embryos have to shift for themselves, and are very active. Here, as in Yoldia, the cilia on each of the three intermediate rows of test cells are



TEXT-FIG. F.—Surface view of a forty-five hour embryo of Yoldia limatula. *ac.* Apical cilia. *bl.* Blastopore. *x.* Depression where the cells that form the cerebral ganglia come to the surface.



TEXT-FIG. G.—Median sagittal section of a thirty-six hour embryo of Yoldia limatula. *ap*. Apical plate. *bl*. Blastopore. *cg*. Cells from which the cerebral ganglia are formed. *mg*. Mid-gut. *sg*. Shell-gland. *std*. Stomodæum. *t*. Test.

long and collected into a band (text-fig. H). Sometimes part of a fourth band is present. The end rows of test cells have the cilia evenly scattered over their surfaces. The apical cilia are long and bunched into a sort of whip that precedes the embryo when it swims. In fact, the embryo resembles that of Yoldia so closely that, except for a difference in size and a slight difference in shape, a description of the surface appearance and movements of one will do very well for the other also.

The cilia on the embryos of Nucula delphinodonta may then be regarded as arrested in their development. Life in the protecting brood-sac makes active locomotion unnecessary and even dangerous, inasmuch as active embryos would be likely to find their way out of the brood-sac, and so be exposed to outside dangers.

The embryos continue to elongate and begin to flatten slightly laterally (fig. 23). In the living embryo, viewed by transmitted light, this stage is marked by the appearance of a light spot near the dorsal margin. A smaller, much less distinct light spot has been present near the ventral margin for some time, and corresponds in position to the cavity that was mentioned as appearing in the mesoderm, ventral to the gut. This space has enlarged considerably (fig. 24), but is covered laterally by rather thick walls of ectoderm and by some mesoderm, so it is not very distinct. The dorsal space is formed by the arching up and flattening out of the cells of the shell-gland, which are now beginning to form the mantle lobes (fig. 20). It is bounded dorsally, laterally, and posteriorly by the mantle, anteriorly by the mantle and the apical plate, and ventrally by the gut and by the body-wall. A few cells, apparently mesodermal, lie in this space, generally attached to the mantle or to the gut.

At a little later stage (fig. 25) two fibre-like cells stretch from the anterior end of the gut posteriorly and dorsally to the mantle. They are quite conspicuous in living embryos, and they retain their position until after the test is thrown away.

About this stage the gut, which has grown posteriorly, acquires an anus (fig. 24). The anus is not directly applied to the pore that opens between the test cells, but it opens into a cavity that is continuous laterally with that portion of the embryo

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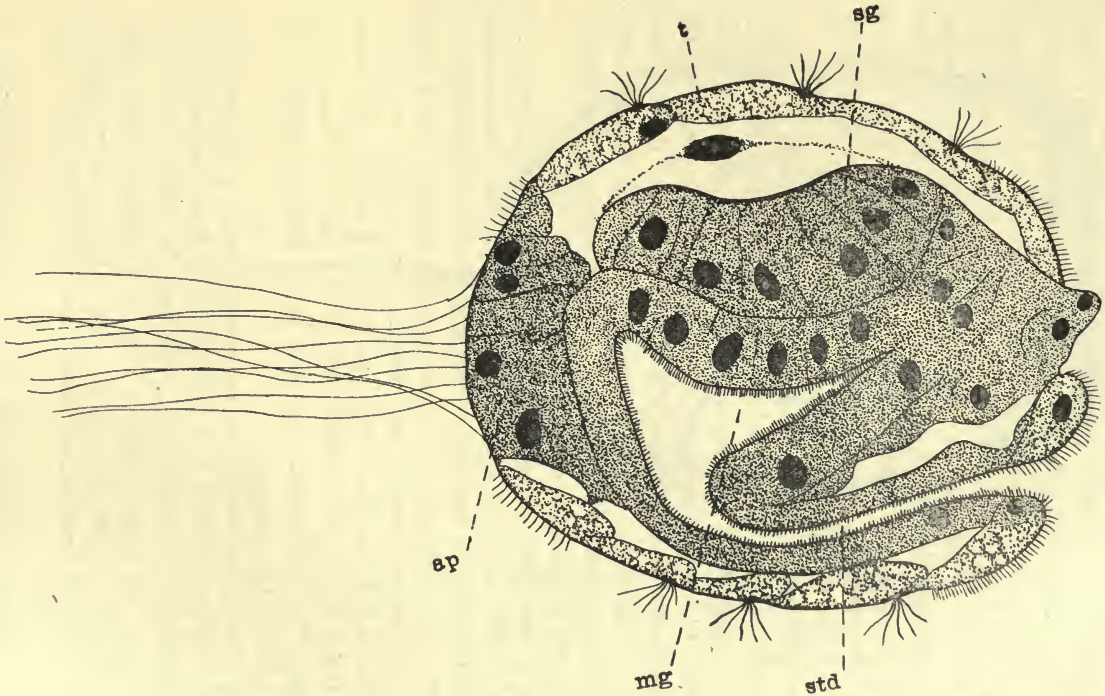


TEXT-FIG. H.—Median sagittal section of a twenty-five hour embryo of Nucula proxima.
ap. Apical plate. *mg.* Mid-gut. *sg.* Shell-gland. *std.* Stomodæum. *t.* Test.

that, as the mantle continues to grow, becomes the mantle chamber. This communication will be described in a later stage.

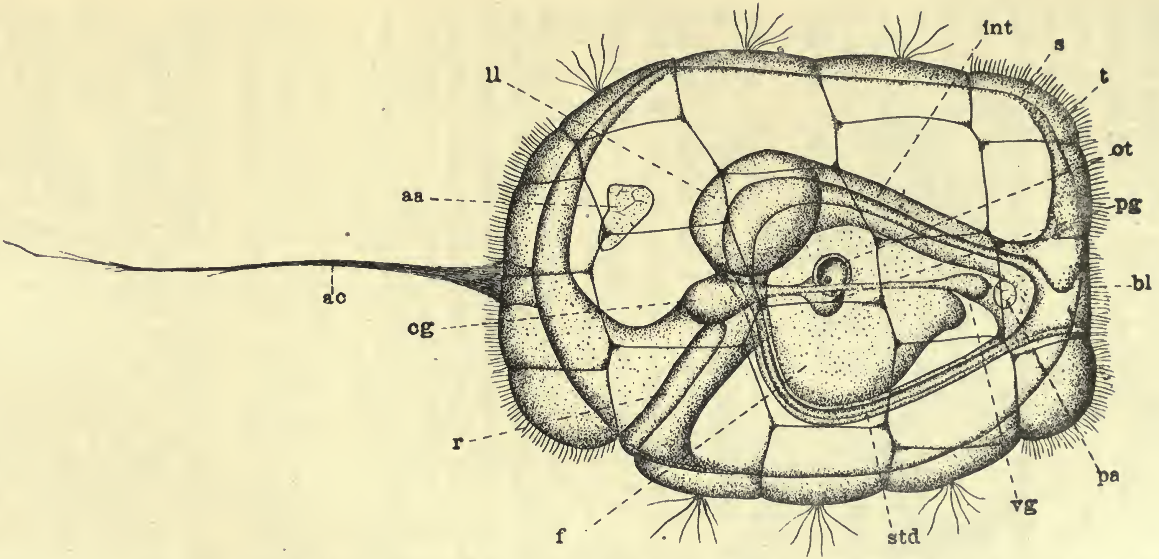
The embryo flattens laterally until its thickness equals about two-thirds of its dorso-ventral width, and the dorsal space becomes considerably enlarged (fig. 25). Near the anterior end of this space the anterior adductor muscle (*aa.*) makes its appearance. At first it consists of a very few fibres, and is not conspicuous. The anterior enlarged portion of the gut takes on the distinctive characters of the stomach (*sto.*), and the liver grows out as paired right and left pouches (*l.*). The anterior end of the stomach is carried dorsally, and a more or less distinct bend is made where it joins the intestine.

The relationship of the various cavities in the embryo to each other, and of the anal pore in the test to the mantle chamber, can be best understood by comparing the sagittal, horizontal, and tranverse sections of embryos, represented on Plate 22, with the reconstruction of an embryo at the same stages of development (Plate 21, fig. 25). The position of the horizontal and transverse sections are indicated on fig. 25 by numbers that correspond to the numbers of the figures.

The dorsal cavity is separated from the ventral cavity by the gut (fig. 28). In some sections the two cavities communicate around the sides of the gut. This may be due to shrinkage, but it seems more likely that the two portions are parts of a single cavity. It is just possible that the cleavage cavity never entirely disappears, and that this cavity can be traced back to the blastocœle, but I am of the opinion that it is a later formation, and represents a schizocœle. Its fate is of interest, and will be referred to in later stages.

The lobes of the mantle are now well formed, a distinct shell-cuticle has been secreted, and some lime salts have been deposited. The stomodæum for most of its length is joined, but is not enclosed by the body ectoderm (fig. 28), which in this region forms the walls of the foot (*f.*). Near its external opening the stomodæum has become free, and is more or less closely joined to the test cells.

The relation of the anal test pore to the mantle chamber can now be understood. As shown by a sagittal section (fig. 26), this pore opens into a small cavity that receives the anus. This

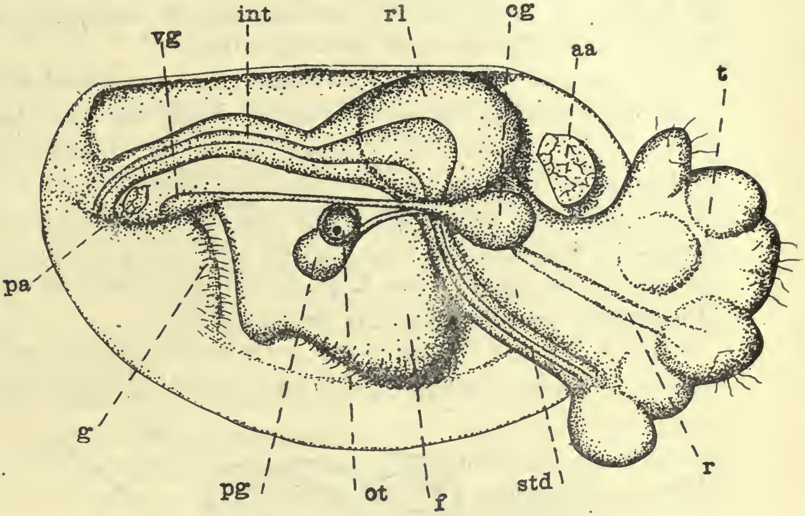


TEXT-FIG. I.—Reconstruction of an embryo of Yoldia limatula at a stage just before the test is cast off. The embryo is seen from the left side. Specimens are .2 mm. long without the apical cilia. *aa.* Anterior adductor muscle. *ac.* Apical cilia. *bl.* Blastopore. *cg.* Cerebral ganglion. *f.* Foot. *int.* Intestine. *ll.* Left lobe of the digestive gland. *ot.* Otocyst. *pa.* Posterior adductor muscle. *pg.* Pedal ganglion. *r.* Pouch leading from the surface to the cerebral ganglia. *s.* Shell. *std.* Stomodæum. *t.* Test. *vg.* Visceral ganglion.

cavity is bounded anteriorly by the posterior wall of the foot, and ventrally either by the stomodæum or by cells covering the dorsal portion of the stomodæum. Transverse (fig. 27) and horizontal (fig. 31) sections show that this cavity spreads out laterally, and becomes continuous with that portion of the mantle chamber posterior to the foot. At this stage the foot is very imperfectly formed, and contains the cavity that has been referred to as the ventral cavity. The cavity soon disappears, and the ectoderm on the two sides of the foot fuse ventrally, dorsal to the stomodæum. The foot is still very small, and shows no sign of its future activity. At a corresponding stage the foot of Yoldia is quite well developed (text-fig. I). This is about the condition of the embryo when the test is thrown away.

It takes several hours for embryos of this species to cast the test, a process that with Yoldia limatula and Nucula proxima is completed within a very few minutes after it is begun. The test cells in the region of the anal pore break apart, and the whole mass is frequently pushed forward to the region of the apical plate. This stripping forward carries the outer end of the stomodæum forward to some such position as is shown by fig. 34. The cilia on the test cells remain feebly active for a considerable time. While the test cells, stomodæum, and apical plate still adhere to the embryo, the stomach and liver pouches are drawn some distance dorsally into the schizocœle (fig. 34, *sto.* and *l.*). Whether the fibres extending from the stomach to the mantle are important in effecting this movement is not known. Their position is suggestive, but I have no direct evidence that they contract. The position now occupied by the stomach causes the bend where the intestine joins the stomach to become quite abrupt.

At the same time that the stomach moves dorsally, the cerebral ganglia (fig. 34, *cg.*), which are still a mass of rather undifferentiated cells, are carried up, and come to lie posterior and a little ventral to the anterior adductor muscle (*aa.*). The foot (*f.*) retains its position beneath the intestine and stomach, and in the general dorsal movement is carried a little further from the margin of the shell. A similar stage for Yoldia is represented by text-fig. J. At the end of several hours the stomodæum (fig. 34, *std.*) breaks across near the tip of the foot, and together with the apical plate and the remnants of the test cells is thrown away. From appearances I am inclined to believe that the whole of the apical plate is thrown away, but this may not be the case. The test cells may or may not remain attached to the apical plate and stomodæum until these are thrown away. Generally many of them break loose or go to pieces before this change occurs, but some of them nearly always remain.



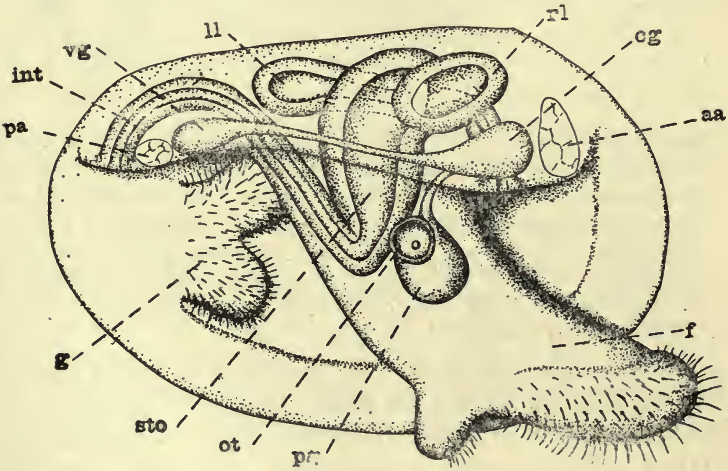
TEXT-FIG. J.—Reconstruction of an embryo of Yoldia limatula at a stage during casting. Represented as seen from the right side, with the right shell-valve and mantle lobe removed. *aa.* Anterior adductor muscle. *cg.* cerebral ganglion. *f.* Foot. *g.* Rudiment of gill. *int.* Intestine. *ot.* Otocyst. *pa.* Posterior adductor muscle. *pg.* Pedal ganglion. *r.* Pouch that leads to the cerebral ganglia. *rl.* Right lobe of the digestive gland. *std.* Stomodæum. *t.* Adhering test cells. *vg.* Visceral ganglion.

After casting is completed (fig. 35) the stomach (*sto.*) and the liver lobes (*l.*) are drawn further into the schizocœle, and the liver lobes begin to be flattened out against the mantle. The cerebral ganglia (*cg.*) lie almost directly posterior to the anterior adductor muscle (*aa.*), and the ectodermal thickenings that result in the formation of the pedal and visceral ganglia soon begin to form (fig. 36).

Thus far in the development of the animal the shell-valves have remained gaping, but after the removal of the apical plate and the stomodæum they are free to close. This is effected by the contraction of the anterior adductor muscle, and materially diminishes the space between the shell-valves.

The closing of the shell is accompanied by important changes in the liver pouches, changes similar to those that have been described for Yoldia (1). Apparently as the result of the mechanical pressure, the liver pouches go to pieces, and the large cells of which they were composed become rounded and scattered through most of the schizocœle (fig. 36, *z.*). The posterior portion of the schizocœle is not filled by the scattered liver-cells. This persists and finally becomes the pericardium.

The foot (fig. 39, *f.*) grows and soon executes feeble movements. The pedal ganglia (*pg.*) and visceral ganglia (*vg.*) take on definite form; the posterior adductor muscle (*pa.*) appears; and the invaginations that result in the formation of the



Text-fig. K.—Reconstruction of a ten-day embryo of Yoldia limatula. Represented as seen from the right side with the right shell-valve and mantle lobe removed. *aa.* Anterior adductor muscle. *cg.* Cerebral ganglion. *f.* Foot. *g.* Gill. *int.* Intestine. *ll.* Left lobe of the digestive gland. *ot.* Otocyst. *pa.* Posterior adductor muscle. *pg.* Pedal ganglion. *rl.* Right lobe of the digestive gland. *sto.* Stomach. *vg.* Visceral ganglion.

otocysts are formed. Very possibly commissures connect the ganglia at this time, but I have not been able to distinguish them from the surrounding tissue until a somewhat later stage. A thickening on the inner surface of the posterior end of each lobe of the mantle indicates the beginning of the formation of the gill (fig. 39, *g.*).

About this time a little invagination on the mid-line of the ventral portion of the foot, just anterior to the heel-like projection, makes its appearance (fig. 39, *bg.*). This develops into the byssal gland. It grows rapidly until it becomes proportionately very large (fig. 45, *bg.*), then ceases to grow, and possibly shrinks somewhat. In the adult it is comparatively insignificant (fig. 48). No signs of byssal threads have ever been observed, nor have the secretions ever been seen to protrude from the duct of the gland.

The foot grows rapidly, and the projection that looks like a heel becomes more marked (fig. 40, *f.*). Anterior to this projection the sides grow ventrally faster than the intermediate portion, and finally form the side flaps that are so characteristic of the foot of the adult. Movements of the foot now become energetic.

The gill (fig. 40, *g.*) becomes more pronounced, and soon unequal growth causes it to be divided into two lobes. The dorsal wall of the stomach re-forms, and the liver-cells begin to be rearranged. The commissures between the ganglia are distinctly visible. The otocysts (*ot.*) are quite large, and contain granules. Although adults have canals leading from the otocysts to the exterior, I have not been able to demonstrate their existence in this or somewhat older stages. The presence of the otocystic canal had been explained (13) as the persistent opening of the otocyst, which was formed as an invagination from the surface of the body. This seems to be the natural explanation, but if canals are present at this stage they are certainly very small. I am inclined to regard the exceedingly small size or absence of these canals as evidence against the view that the otoliths are foreign particles.

Thus far most of the embryos have been carried in the brood-sacs, but many of them now become free. They are not set free by any act of the mother, but they individually find their way into the mantle chamber of the mother and so to the exterior.

Frequently younger embryos become free, but they generally do not live long. Many embryos remain in the brood-sacs until a much later period, but they do not seem to be in need of its protection after the stage that has just been described. The brood-sacs frequently remain intact after all of the embryos have left them.

The more dorsal of the gill lobes elongates into a finger-like process, and the ventral lobe broadens and becomes divided into two lobes (fig. 41, *g.*). New lobes are thus formed as the result of unequal growth of the most ventral lobe.

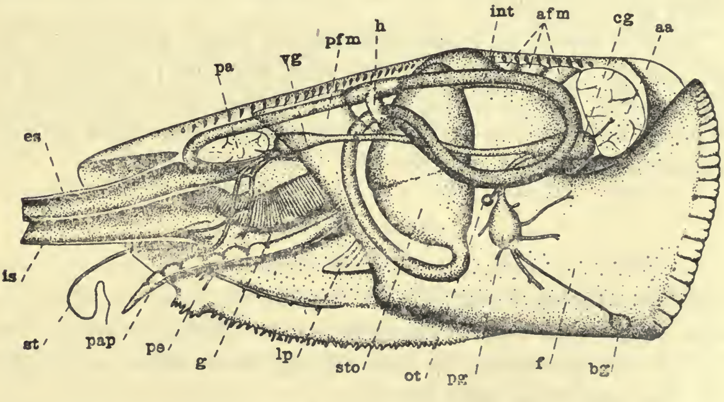
About the time that the third lobe of the gill begins to form, a few papillæ appear along the margins of the side flaps of the foot (fig. 41, *f.*). The liver lobes also become hollowed out and lose most of the rounded cells. Part of these cells seem to go to pieces much as if digested (fig. 43), and it seems quite possible that this is the case.

The heart (fig. 41, *h.*) is apparently formed from mesodermal tissue that collects to form a strand, that runs across the pericardium from one side to the other. I have found no indication of its being formed as paired pouches, as described by Ziegler (20) for Cyclas cornea, nor have I found any evidence that it originates as two masses that grow toward each other. Its first appearance seems to be in the form of a mesodermal strand of tissue that soon hollows out and encloses the intestine. The fact that the heart forms around the intestine, and not dorsal to it, is of interest, and will be discussed under the head of the Circulatory System.

The growth of the kidneys, which are now present as small tubes, seems later to force the sides of the heart up around the intestine (fig. 68), so that the ventral portion of the ventricle becomes drawn out into a trough in which the intestine lies. As the kidneys grow the trough becomes deeper. By gradually closing in dorsal to the intestine at the anterior and posterior ends, the trough is shortened, and the intestine finally becomes free from the heart and lies ventral to it (fig. 69). This is accomplished by a very slow process, and is not completed until after the animal has become sexually mature.

I am inclined toward the opinion that the kidneys are formed by the differentiation of mesodermal tissue. When they first appear each is a very narrow tube, and extends from its external opening in the mantle chamber to the mid-line of the body. I have not succeeded in demonstrating the inner, pericardial openings, of the kidneys in this or in later stages. The cells soon become large and vacuolated, and the kidneys grow rapidly and crowd anteriorly ventral to the pericardium, where they become coiled and sacculated.

With the formation of the fourth lobe of the gill (fig. 45) processes make their appearance on the bases of the lobes, between them and the mantle lobe to which the gill is attached. These processes grow to form what have been called the outer gill plates, but in this species their position is better described as posterior than outer. The lobes, at the bases of which the outer plates are formed, develop into the inner plates. Viewed from the side, both sets of plates are visible. The gills of Yoldia hang so that in a side view the outer plates hide the inner plates, which lie directly behind them (text-fig. L). When viewing Nucula from the side we see that portion of the gill that corresponds to the ventral portion in Yoldia.



Text-fig. L.—Adult specimen of Yoldia limatula. Represented as seen from the right side. Reconstructed to show internal organs. Fully grown specimens may be 6 cm. long. *aa.* Anterior adductor muscle. *afm.* Anterior foot muscles. *bg.* Byssal gland. *cg.* Cerebral ganglion. *es.* Exhalant siphon. *f.* Foot. *g.* Gill. *h.* Heart. *int.* Intestine. *is.* Inhalant siphon. *lp.* Labial palp. *ot.* Otocyst. *pa.* Posterior adductor muscle. *pap.* Palp appendage. *pe.* Posterior expansion of the margin of the mantle. *pfm.* Posterior foot muscle. *pg.* Pedal ganglion. *st.* Siphonal tentacle. *Sto.* Stomach. *vg.* Visceral ganglion.

The labial palps appear as patches of cilia on embryos with three gill lobes (fig. 41). The outer palps soon begin to grow out as flaps (fig. 45, *lp.*), and by the time that the fifth pair of gill plates are formed the inner palps are present as folds. The formation of the ridges on the ciliated surfaces of the outer palps begins with embryos having six pairs of gill plates, and the palp appendages are formed soon after (figs. 55 and 56). The development indicates that each palp appendage (fig. 56, pap.) is to be regarded as a pair of ridges with an enclosed groove, developed and modified so that it may be extended beyond the edges of the shell.

Little remains to be described in this general sketch of the development, further than to call attention to the formation of the loops of the intestine, that are indicated in different stages of development by text-figs. M to S; to the formation of the cartilage pit and teeth on the valves of the shell; to the formation of more gill plates and foot papillæ as these organs continue to grow; to the appearance of the otocystic canals about the time that the sixth pair of gill plates are formed; and to the formation of the genital organs.

Mention should be made of a peculiar closed pouch (figs. 40, 48, and 63, *v.*), of unknown function, that lies just anterior to the anterior adductor muscle. It makes its appearance in embryos that are just getting the second gill lobes, and is fairly conspicuous in adult animals.

GERM LAYERS.

An almost spherical embryo is formed as the result of the first few cleavages (fig. 5), the cells on one side of which are much larger than those on the other side. The large cells extend far into the interior of the embryo, and the smaller cells form a cap over the larger ones (fig. 4).

In reaching this stage of development the embryo has passed through a blastula stage, in which the cleavage cavity was very small (fig. 3). As the cells become arranged in the manner described, the greater part of the cleavage cavity disappears. It has not been determined whether any of it remains or not. A depression appears near one side of the group of larger cells at a point corresponding to the asterisk in fig. 4. This depression seems to be formed by the separation and further division of some of the large cells, and results in the formation of the gut (fig. 8, *mg.*).

The surface cells may now be regarded as ectoderm, and at least two kinds may be distinguished: small ones, which finally form the test, the apical plate, the cerebral ganglia, the stomodæum, and a considerable portion of the future ectoderm of the embryo; and large ones that form the shell-gland.

The endodermal pouch is carried further into the interior by the division and pushing in of ectodermal cells in the region of the blastopore (figs. 9 and 11, *mg.*). In this way a long stomodæum is formed on the ventral side of the developing embryo. The ectodermal covering of the later embryo, exclusive of that derived from the shell-gland, seems to be formed in connection with the formation of the stomodæum, by cells that wander in from the region of the blastopore, and perhaps from the cells derived from the stomodæum itself.

About the time that the stomodæum begins to form, a few cells, two of which are quite large and conspicuous, make their appearance by the sides of the endodermal pouch, and extend between it and the shell-gland. These are mesodermal cells. Their exact origin has not been traced. As the embryo elongates, the two large cells come to lie near the posterior end of the embryo (fig. 19). They probably correspond to similar cells that have frequently been described for other forms. Similar cells are found in Yoldia in a corresponding position.

TEST.

As the result of the first few cleavages a number of large cells become covered on one side by a cap of smaller cells (fig. 4). A part of the smaller cells become covered with cilia, about the time that the gut is formed (fig. 8); others near the blastopore divide rapidly and form the stomodæum (figs. 9 and 11); still others form the cerebral ganglia; while others in the region of the blastopore wander in and form a part of the future ectoderm.

The cells that bear cilia are concerned in the formation of the test and apical plate. These cells soon cover the surface that is not occupied by the shell-gland and the cerebral ganglia.

Both the apical plate and the cerebral ganglia are small at this stage, consist of a very few cells, and can hardly be distinguished from the surrounding cells. The apical cells acquire cilia about the time that the test cells do (figs.9 and 11), and for some time they cannot be distinguished from them. Later the apical plate may be told by its shape and position (figs. 15 and 24, *ap.*).

As development proceeds the test begins to close in over the shell-gland from the sides and anterior end (figs. 10—13). Five rows of test cells can now be seen under favorable conditions, but their outlines are very hard to determine. Until the shell-gland is covered, two or three of the posterior rows are incomplete dorsally. A small pore is left near the posterior end, separated from the blastopore by the width of one test cell (fig. 15). The anus comes to lie near this opening (fig. 24).

The five rows of cells are now arranged much as shown in text-fig. E. From the formation of the test until its ultimate disappearance its cells are evenly ciliated with short cilia. In this respect the embryos differ from those of Yoldia limatula (text-fig. F) and Nucula proxima (text-fig. H). Both of these forms have the cilia on each of the three intermediate rows of test cells collected into a band. Sometimes a fourth more or less complete band is present. The cilia on the end rows of the test cells of all of the forms are short and evenly scattered over the surfaces of the cells.

In this connection it is of interest to observe that the cilia on the apical plate of Nucula delphinodonta are short and independent, while those on the apical plates of Yoldia limatula and Nucula proxima are long and bunched together. They all seem to have a rather scattering origin, and when animals are killed the cilia become separated from one another.

In both species of Nucula the embryo differs from that of Yoldia limatula in having a posterior opening in the test, dorsal to the blastopore (fig. 15, and text-figs. G and H). This difference might easily be accounted for by a slight difference in the closing in of the test over the shell-gland.

The ciliated embryos of Nucula delphinodonta, unlike those of the other two forms, are not able to swim freely in the water. At the most they are barely able to move on the bottom of a glass dish. This is probably the result of their being carried in a protecting brood-sac. It seems but natural that the bands of strong cilia and the apical tuft of cilia would not be developed by embryos such as these, where there is no need for active locomotion, and where active locomotion would be dangerous. It is for the best interest of embryos that they remain in the brood-sacs, where they are protected from many enemies. Were they capable of active movement, many would probably escape and perish. In the two related forms, Nucula proxima and Yoldia limatula, the embryos have to depend on their own activities for their existence.

It is highly probable that the embryos of the ancestors of Nucula delphinodonta led an active, free-swimming existence. The rearing of embryos in protecting brood-sacs is very possibly connected with the present life of the animal beneath the surface of the mud, and, in any case, has probably been acquired at a comparatively recent day. Again, the test in its present condition is of no appreciable value to the embryo, and no doubt is to be regarded as a vestige of a once functional organ.

Young embryos of Nucula delphinodonta when taken from the brood-sacs do not live well, and it is accordingly difficult to determine how long the test is retained. As near as could be judged, it seems to be retained about two weeks. Its cells then begin to break apart near the posterior end of the embryo, and many of them move toward the anterior end, where they remain attached to the apical plate and the stomodæum (fig. 34). Sometimes most of the cells of the test seem to accumulate at the anterior end, but they frequently become detached and go to pieces before reaching this position. In any case they, together with the apical plate and the stomodæum, to the position of the future mouth, are finally thrown away (fig. 35). In many cases the process of casting occupies several and sometimes as many as fifteen hours. The process is much more rapid for both Yoldia limatula and Nucula proxima (2). It is quite possible that the difference in the length of the time occupied by the different embryos is connected with the difference in the conditions under which they develop.

Further study has tended to confirm my view that the test should be regarded as the homologue of the velum of other forms. In a former publication (1) I made the statement that "in either Dentalium or Patella, if we imagine the velum to be stretched posteriorly over the shell-gland dorsally, and the foot ventrally, so as to enclose the body, the œsophagus will be pulled out into a narrow tube ventral to the foot, and the position of the blastopore will correspond to its position in Yoldia. Furthermore the position of the foot and shell-gland will correspond, and the alimentary canal will be bent in the same way." This states the case backward, and may be a little confusing. If we begin with the condition found in Yoldia and Nucula, and imagine the test to shrink until it consists of a band of ciliated cells surrounding the embryo anterior to the mouth, the condition would be comparable to that shown by embryos of Dentalium and Patella.

As in the case of Yoldia, the closest resemblance to the test, outside of the group, is shown by Dondersia. Although Pruvot's (15) account of these embryos is very short, and only three figures are given, there is quite a striking external resemblance. In both cases the surface cells are arranged in five rows, all of which bear cilia. They are both provided with apical plates, and with both the test is finally thrown away. The bodies of the embryos of Dondersia protrude posteriorly during development. A slight posterior protrusion of the body of Nucula sometimes takes place through the opening dorsal to the blastopore.

The resemblances shown by embryos of Dentalium (8 and 9) and Patella (12) are not so striking, but they are somewhat similar. The apparent posterior protrusion of the body in each of these forms is such as might be produced if the body of Nucula were to grow and protrude to a corresponding extent. In such a case the test of Nucula would occupy a corresponding position to that occupied by the velum in the other forms.

APICAL PLATE.

At an early period the cells of the apical plate cannot be distinguished from those that form the test, but as development proceeds they become marked off as a rather definite plate at the anterior end of the embryos (figs. 11; 15, and 24, *ap.*). This plate is relatively large and thick, and extends posteriorly as far as the stomach. The cells from which the cerebral ganglia are formed lie venral to it (figs. 15 and 24, *cg.*). Beneath the test the cerebral ganglia and the apical plate are in contact.

The cells of the apical plate are evenly ciliated with short cilia, like those borne by the test cells (fig. 15). In this respect this species differs from both Nucula proxima and Yoldia limatula. Both of these forms have long apical cilia (text-figs. G and H) that during life are bunched together (text-fig. F). Nucula proxima has an apical plate that in extent may be compared to that of Nucula delphinodonta, but the apical plate of Yoldia is comparatively very small. The short, diffuse cilia on the apical plate of Nucula delphinodonta are probably the result of the conditions that make active locomotion at this stage both unnecessary and dangerous. (See what is said regarding this under the head of Test.) Certainly most of the apical plate, and probably all of it, is cast away when the test is shed (figs. 34 and 35).

SHELL.

Some lime salts are deposited soon after the cuticle of the shell begins to be secreted, which takes place about the time that the lobes of the mantle begin to form (fig. 20). When the test is shed (figs. 34 and 35), the shell-valves are white, glossy, and quite transparent. They do not correspond to the adult valves in shape (fig. 50), and they do not have the long, straight hinge-line of the prodissoconch of Yoldia (text-fig. K). The hinge-line is not very definitely marked off from the rest of the shell, but it can be distinguished as a nearly straight or slightly curved portion on the dorsal margin (fig. 36). The difference in the shape of the prodissoconches of Nucula and Yoldia is quite marked, more marked than might have been expected for forms so closely related, when there is so much resemblance between the prodissoconches of many Lamellibranchs (6). They both conform to the same type, however.

At first the valves are thin and have neither cartilage pit nor teeth. Soon after casting, a little knob of cartilage (fig. 36, *ca.*) makes its appearance near the middle of the hinge-line. The teeth do not form until a much later stage (fig. 46). About the time that the fifth pair of gill plates are formed, a tooth appears on each valve in front of the cartilage pit. This is soon followed by another, which is added anteriorly. The teeth posterior to the cartilage pit begin to appear about the time that the third tooth anterior to the cartilage pit is formed. New teeth in the posterior series are added posteriorly. Only about half as many teeth are formed posterior to the cartilage pit as anterior to it. Apparently as long as the shell continues to grow in size new teeth are added. Shells of fully grown specimens are about 4 mm. long, but they sometimes occur nearly 5 mm. long.

Each shell-valve is very convex (figs. 50 and 51), slightly oblong, and moderately thick. The beaks are directed posteriorly and placed far back on the shell. This gives an appearance quite the reverse of most Lamellibranch shells, which have the beaks nearer the anterior than the posterior ends, and directed forward. The cuticle of the shell differs in different specimens from horn colour to dark brown or nearly black. It may be considerably broken near the beaks, but it is generally quite perfect and smooth. Unlike most Lamellibranchs, the shells of this species contain so much animal matter that they retain their forms after the lime salts have been dissolved away. The material is quite tough, and frequently causes much trouble in cutting series of sections.

Each valve of the shell of fully adult animals has from ten to twelve teeth in the series anterior to the cartilage pit and five or six posterior to it (figs. 50 and 51). All of the teeth are more or less conical, pointed, curved toward the dorsal margin of the shell, and distinctly grooved on the side away from the cartilage pit. Each series of teeth forms a ridge some distance from the dorsal margin of the shell, which disappears dorsal to the adductor muscle-scar. The teeth of the two valves interlock so completely that it is frequently quite impossible to separate the valves without breaking some of them. The cartilage pit is large and deep. The adductor muscle-scars and pallial lines are faintly marked.

The shell-gland is formed early. About the time that the gut is formed it consists of a number of large cells that lie near the blastopore, on what may be distinguished as the dorsal side of the embryo. Its cells do not seem to bear cilia, but only preserved material was at hand for the determination of this point. The surrounding ciliated cells, those that form the test, begin to grow over the shell-gland from the sides and anterior end (figs. 10, 11, 12, and 13, *sg.*). At the same time the shell-gland flattens slightly, and the cells along its margin push up and form a slight ridge, that keeps the surface of the shell-gland separated from the overgrowing test. Soon after the shell-gland is covered by the test, it arches dorsally, and the two come to lie close together (figs. 17 and 18, *sg.*). As the embryo flattens laterally the shell-gland arches dorsally still more (fig. 20), and a space appears between it and the intestine. This space seems to be formed by the multiplication and flattening of the cells of the shell-gland, which arches dorsally and becomes separated from the intestine. Lateral folds (fig. 20, *m.*), the beginnings of the mantle lobes, are soon formed. About this time the shell cuticle is secreted and some lime salts are deposited.

Soon after casting has been completed, swellings, the beginnings of the gills (fig. 39, *g.*), are formed near the posterior margin of each lobe of the mantle. The gills are thus formed as appendages of the mantle.

The mantle now has the adult structure and appearance, except that at a later stage a portion of its inner epithelium, and of the epithelium covering the suspensory membranes of the gills, becomes converted into the hypobranchial glands. These glands are present in both sexes, but just before the breeding season they are much better developed in the females than in the males, and there is considerable evidence that they furnish most, if not all, of the material from which the brood-sacs are formed. The margins of the mantle lobes remain thickened and contain the glands that secrete the cuticle of the shell. Some cells along the ventral and posterior borders of the mantle lobes bear cilia. Pallial muscles are attached to the shell-valves, and extend out to the margins of the mantle. These serve to retract the margins of the mantle when the shell is tightly closed.

FOOT.

At a stage such as is represented by figs. 14 and 15, a group of cells lie between the gut and the stomodæum. These cells, together with the ectodermal side walls, are concerned in the formation of the foot. The side walls of the foot are continuous with the general ectodermal covering of the body beneath the test. The cells lying between the gut and the stomodæum are apparently mesodermal, and enclose a small space (figs. 15 and 24). The shell-gland spreads out, arches dorsally, and folds laterally to form the mantle, and a large space is left between it and the stomach and intestine (figs. 20, 24, and 26). In some transverse sections the space between the stomodæum and the intestine, and the space dorsal to the intestine, are more or less connected. This connection may be due to shrinkage caused by preservatives, but it seems probable that the two spaces are naturally more or less definitely connected around the sides of the stomach and intestine, and that they may be regarded as a single cavity—a schizocœle.

The side walls of the foot join the stomodæum, and are not continuous with each other ventrally (figs. 20 and 28). Just before the test is cast away they begin to unite dorsal to the stomodæum, and the stomodæum becomes comparatively free. This change begins at the posterior end of the foot and works forward.

The process of casting is slow, and includes a large part of the stomodæum. When it is completed, the foot consists of a small mass of tissue, lying ventral to the stomach and intestine (figs. 34 and 35, *f.*). It is not capable of executing movements, and for a period of about a day, or even longer, the embryo lies perfectly quiet with the shell-valves tightly closed. At first I supposed that this comparatively immature condition of the foot at the time of casting was connected with the protected life of the embryo. The foot of Yoldia executes movements before the test is shed, and burrowing is begun almost as soon as the process is completed. It seemed natural to conclude that the greater development of Yoldia at this time depended upon the necessity for self-preservation. It was surprising, then, to find that at a corresponding time the foot of Nucula proxima is no better developed than is the foot of Nucula delphinodonta. This seems very remarkable to me, for Nucula proxima inhabits muddy and shelly bottoms over which flow quite strong tidal currents. Under these conditions it would seem that such perfectly helpless embryos would surely perish.

The foot of Nucula delphinodonta grows rapidly, and by the second day (fig. 36) performs feeble movements, but it is not thrust out of the shell for some time. It becomes provided with cilia (figs. 39 and 40), but they are not as powerful as those on the foot of Yoldia (text-fig. K), and they are of but little service in locomotion.

The first movements of the foot are feeble twitches. These in time become more frequent and powerful. Finally the foot is thrust out of the shell, stretched ventrally and anteriorly, swelled up at the end, and held more or less rigid while the cilia vibrate. After being held in this position for a few seconds it is withdrawn, either to remain quiet for some time, or to be immediately thrust out again. The earlier movements are not very energetic, and as the side flaps have not been formed, they are not like the movements of the adult.

The first indication of the side flaps consists of a slight longitudinal groove on the mid-line of the ventral surface of the foot. On each side of this groove the foot grows to form flaps (figs. 40 and 61) that lie side by side.

Soon after the test is shed, a rounded knob develops on the postero-ventral portion of the foot (fig. 36). This grows quite rapidly, and forms the prominence that appears like a heel (figs. 40 and 41). It soon stops its rapid growth, and in the adult is comparatively small (figs. 48 and 49). In this species it is comparatively much larger in the adult animal than in any of the other species that I have studied.

The side flaps at first have smooth margins (fig. 40), but papillæ soon begin to be formed (fig. 41). The anterior papillæ are formed first, and new ones are added posteriorly as the foot grows, until as many as thirteen pairs have been formed (fig. 48). The number differs with the size of the individual. Sexually mature specimens may be found with no more than eight pairs. The papillæ are large, conical, more or less pointed, and very sensitive to mechanical stimulation.

The movements of the foot of this species when compared with the movement of the foot of Yoldia are very deliberate, but the foot is so large, and the muscles so powerful, that burrowing is quite rapid. Individuals of this species seem normally to live entirely covered by mud, in which they wander around by slow thrusts and retractions of the foot. Specimens do not seem to come to the surface of the mud to remain for any considerable time, and it seems probable that the greater part of the lives of individuals are passed beneath the surface of the mud. Observations made on specimens kept in dishes of sea water in which there was no mud show that individuals of this species execute movements very similar to those executed by Yoldia (1), but that in all cases they are much more deliberate (3). Leaping movements are absent, but slow thrusts with the flaps extended may frequently be observed. In former publications attention has been called to the characteristic movements of the foot, and they need not here be redescribed (1 and 3). As in the case of other members of this group, the movements of burrowing are very effective. The somewhat spherical shape of the shell, and the relatively large size of the foot, make it possible to raise the shell from the bottom of a dish, and occasionally to keep it balanced for a few seconds over the expanded foot. My observations lead me to believe that the animals never creep.

As in Yoldia, the foot is supplied with complicated and powerful muscles (1 and 3). It is attached to the shell by three pairs of muscles, and by a few fibres that lie ventral to the genital mass and liver. The posterior pair of foot muscles is very powerful. These muscles are attached to the shell at the bases of the teeth, just anterior to the posterior adductor muscle, and extend along the sides of the foot in an anterior and ventral direction. They are the powerful retractor muscles of the foot. Fibres from them are extended into the muscular flaps, and are important in spreading them apart.

The two anterior pairs of foot muscles correspond to the three anterior pairs of foot muscles in Yoldia. They are inserted on the shell close together along the bases of the teeth, just posterior to the anterior adductor muscle. The more anterior pair has much the same distribution as the two anterior pairs in Yoldia, and in some cases each muscle seems to be slightly separated into two near its origin. They spread out along the sides of the foot, and are distributed to its posterior and ventral portions. These muscles seem to be closely connected with the muscle-fibres that are attached along the sides of the shell ventral to the genital mass and liver. The more posterior of the two anterior pairs of foot muscles passes between the pair just mentioned, and is distributed to the anterior and ventral portions of the foot.

In the foot all of the muscles are closely bound together by their own fibres and by interlacing fibres, so that many movements occur that cannot be explained by direct pulls of individual muscles. It should constantly be borne in mind that the attachments of the fibres are all along the sides of the foot, and that many, if not most of the muscle-fibres pull from one portion of the body-wall to another, without changing the relation of the body to the shell. Thus the flaps can be spread apart after the shell has been removed. By compressing the blood contained in the large spaces of the foot, many movements, especially those connected with protruding the foot, may be performed.

As in the case of Yoldia, the foot muscles are so large that they are attached along a considerable portion of the dorsal surface of the shell. I regard this as the result of the size of specialised muscles, and do not agree with Pelseneer (13) that it should be regarded as a primitive character.

BYSSAL GLAND.

The byssal gland is formed as an invagination, just anterior to the posterior projection of the foot, about the time that the side flaps of the foot begin to form (fig. 39). Although there is but a single external opening, the gland at first consists of right and left pouches that extend into the foot near its posterior side. The cells forming the upper portion of the gland soon become somewhat swollen, and do not stain very well with hæmatoxylin. The lumen of the gland soon shows traces of a secretion, but the secretion has never been seen protruding from the duct.

The gland soon enlarges to a remarkable extent, becomes quite irregular, and the paired appearance disappears. At this stage, which extends from about the time that the gill acquires its third lobe (fig. 41) until about the time that it acquires its fifth pair of plates (fig. 45), the byssal gland extends through a considerable portion of the foot, and in the posterior side of the foot it may extend to a position somewhat dorsal to the pedal ganglia. The cells of the gland during this stage are greatly swollen and vacuolated, and have thin, almost indistinguishable walls. They are crowded together so as to almost obliterate the lumen of the gland. The result is that stained sections of the gland have the appearance of a fibrous or recticular mass that is so mixed up as to be hardly intelligible.

As the embryo gill begins to acquire its fifth pair of plates the byssal gland generally becomes less extensive. In the adult it is reduced to a small pouch (fig. 48, *bg.*) that opens in the median groove of the foot, just anterior to the heel-like projection. The dorsal, blind end of the pouch consists of comparatively large cells with small nuclei, and seems to be secreting. They are not generally distended with secretion, and the duct is generally quite empty. Nothing comparable to byssal threads have been observed. Towards the opening of the gland the cells become smaller and bear cilia.

I have described the adult condition that seems most frequently to prevail. In a few specimens the gland cells are much shrunken, and seem to contain little or no secretion. In some specimens of Nucula proxima the gland is more extensive and the cells are greatly distended. This would seem to indicate that the gland is functional, but not as an organ for the formation of threads. The present use of such a secretion is problematical.

It is very natural to compare this gland to the mucus-secreting glands of Gastropoda, but there seems to be little direct evidence that they are homologous.

ALIMENTARY CANAL.

There is a stage when the embryo resembles an epibolic gastrula (fig. 4). A pouch appears between the large cells, at a point corresponding to the asterisk, that seems to be formed by the separation of some of the larger cells, accompanied by their division into smaller cells. This pouch is the first indication of the alimentary canal (fig. 8, *mg.*). Partly by the division of cells forming it, and partly by the addition of ectodermal cells around the blastopore, the gut is carried further into the interior (figs. 9 and 11), and comes to lie at the end of a narrow tube, the stomodæum (fig. 15, *std.*). The blastopore never closes, so from its first appearance the stomodæum is connected with the gut.

The blind end of the gut turns dorsally beneath the shell-gland (fig. 11, *mg.*), and soon begins to grow posteriorly (fig. 15, *int.*). It finally comes to the surface at the posterior end of the embryo at a point ventral to the shell-gland and dorsal to the blastopore (fig. 24), where the anus is formed. The anus does not open directly to the exterior, but opens into the mantle chamber near an external opening in the test.

The alimentary canal at this stage consists of three distinct parts (fig. 24): a slender tube, the stomodæum (*std.*), opening through the blastopore and extending forward nearly to the apical plate, that is formed from the ectoderm; a rather thick-walled stomach (*sto.*) that lies dorsal to the anterior end of the stomodæum, and ventral to the shell-gland; and the intestine (*int.*), which joins the posterior end of the stomach, and at first has rather thick walls.

Dorsal to the stomach and intestine, between them and the shell-gland, a cavity makes its appearance that communicates by lateral passages with another cavity that lies ventral to the stomach and intestine, between them and the stomodæum. The ultimate fate of these cavities has been referred to in the sketch of the life-history, and in connection with the foot, and will again be referred to in connection with the pericardium. For some time they are rather large, and a portion of the alimentary canal is left quite free from surrounding tissue, except where it seems to rest on the walls of the developing foot (fig. 28). A short time before the test is shed the liver pouches make their appearance (fig. 25, *l.*). These are formed from the sides of the anterior end of the stomach.

The cells of the epithelial walls of the stomach are of two kinds. Those at the anterior end of the stomach carry comparatively few cilia, and those at the posterior end carry many cilia. At this stage some of the cells on the dorsal side of the stomach, near its anterior end, begin to secrete a mucus-like material that extends posteriorly in the lumen of the stomach as a small rod that probably represents the crystalline style (fig. 26). Later the posterior portion of the whole dorsal division of the stomach (the part that at this stage is the dorsal part of the anterior portion) is given over to secreting this material, but a definite rod may not be present.

About the time that the embryo casts its test the stomach grows dorsally into the space above it, so that a ventral bend is formed where the stomach joins the intestine (fig. 26). This is the beginning of the abrupt bend that marks this portion of the alimentary canal in later life. Two fibre-like cells stretch across the dorsal space from the anterior end of the stomach to the mantle (fig. 25). Their position suggests that they may aid in moving the stomach into the more dorsal position, but there is no direct evidence that this is the case.

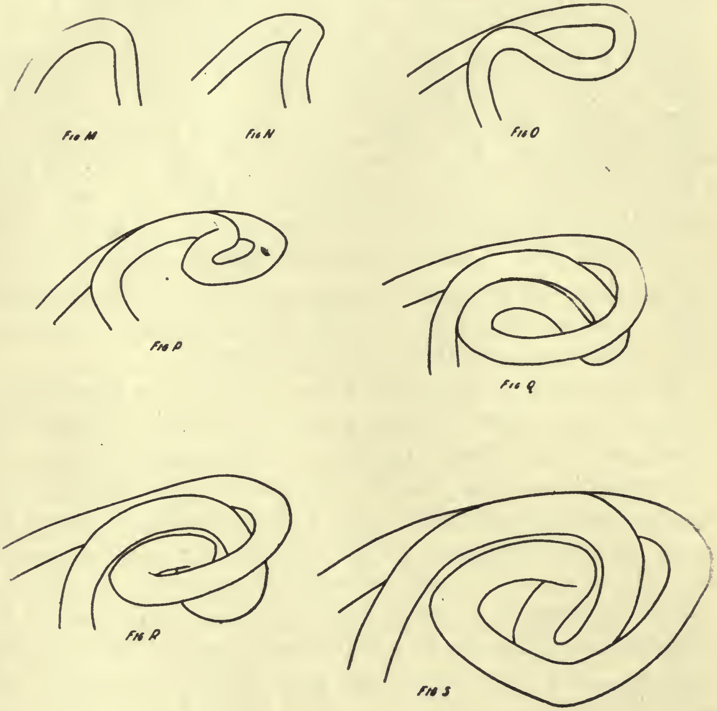
When the test is cast away and the adductor muscle pulls the shell-valves together, the stomach is crowded further into the dorsal space, and the bend in the intestine becomes more pronounced (figs. 34 and 35). The same pressure apparently causes the liver pouches to go to pieces. Their cells become more or less separated, and fill the larger part of the cavity dorsal to the stomach (figs. 36—39, *z.*). The same changes have been noticed in embryos of Yoldia limatula and Nucula proxima. In all of these forms the changes occur in connection with the closing of the shell. Until the test is shed, tissue lies between the valves of the shell so that they cannot be shut together. When the tissue is removed, and the shell is closed, there is no longer room for the liver pouches to lie on the sides of the stomach and retain their original shape. They are accordingly flattened and pressed into the unoccupied space dorsal to the stomach. The cells are no longer arranged to form definite walls (figs. 36—39, *z.*), but later some of them seem to form liver pouches again (figs. 42—44). A small portion of the space into which the stomach and liver are crowded is not filled, and finally forms the pericardium (figs. 39—41).

The rupture of the liver pouches leaves the dorsal part of the stomach without side walls, and the dorsal wall is commonly broken (figs. 37 and 39). The dorsal wall is formed again before the liver pouches regain their cavities (fig. 40). Some of the separated liver cells find their way into the open stomach (figs. 37 and 38), and together with mucus practically fill it.

For a period of two or three days after casting, the animal is not active, and it is doubtful if it feeds. At the end of this time the walls of the stomach begin to re-form, and the mass of material that has filled the stomach has largely disappeared. For a number of days the liver does not form definite pouches. The rounded and scattered cells are finally collected into two masses (figs. 40 and 42) that finally form new liver lobes. The left is slightly larger than the right mass, but the masses are more nearly equal in size than is the case with Yoldia. In both cases it seems that the difference in the size of the two liver lobes causes the developing loops of the intestine to take up a position on the right side. Cavities gradually extend out into the liver pouches from the stomach (figs. 43 and 44). In the formation of the cavities some of the rounded cells seem to go to pieces in much the same way as they would if digested.

The elongation of the intestine that results in the formation of the loops begins about the time that the embryo acquires its fourth pair of gill plates (fig. 45). This elongation carries the portion of the intestine that lies dorsal to the posterior adductor muscle toward the posterior wall of the stomach and nearer the dorsal margin of the shell. The end of the loop is forced over to the right side, and is extended anteriorly nearly to the anterior wall of the stomach. At this stage (text-fig. O) the loop of the intestine is much like the loop that occurs in adult Yoldia limatula (text-fig. L). The dorsal bend now begins to elongate and project anteriorly (text-fig. P). This continues until the loop is extended between the limbs of the loop that was made first (text-fig. Q). The lower limb of the loop begins to elongate (text-fig. R), and the adult condition is soon reached (text-fig. S and fig. 48).

The heart makes its appearance some time before the loops of the intestine begin to be formed (fig. 41). From the first appearance of its cavity the heart surrounds the intestine. This condition continues for a long time, until the loops of the intestine have been formed, and, in fact, until after the animal has reached sexual maturity. At first the intestine passes through the middle of the heart (fig. 67). The sides of the heart seem later to be forced dorsally by the growth of the kidneys, and the intestine becomes applied to the ventral wall of the heart. By the continued growth of the kidneys the ventral portion of the ventricle is drawn out into a trough, in which the intestine lies (fig. 68). The growth is continued until the trough is considerably deeper than the width of the intestine. By gradually closing in dorsal to the intestine at the anterior and posterior ends the trough is shortened, and the intestine finally becomes free from the heart and lies ventral to it (fig. 69).



TEXT-FIGS. M, N, O, P, Q, R, AND S.—Stages in the development of the loops of the intestine in Nucula delphinodonta.

In the adult animal (fig. 48) the œsophagus is a rather broad and long, nearly cylindrical tube, that opens between the palps just posterior to the anterior adductor muscle. I find no indication of anything that can be interpreted as salivary glands at any stage in the development (13). Throughout its length it is evenly ciliated and quite devoid of ridges. The corners of the mouth are continuous with the groove between the two labial palps. The stomach is large, somewhat spindle-shaped, and extends from near the dorsal margin of the shell to the level of the pedal ganglia. Near its middle there is a nearly complete ridge of elongated epithelial cells, and frequently a more or less well-marked external groove that divides it into a dorsal and a ventral portion. The posterior and part of the lateral walls of the dorsal portion of the stomach are formed by long and slender epithelial cells that stain but slightly. They secrete a mucus-like material that stains deeply, and probably corresponds to the crystalline style. In adults this secretion seldom takes the form of a rod, but in embryos a rod is commonly present (figs. 26, 28, 30, and 64). The remaining cells in the dorsal portion of the stomach are short, stain deeply, and are evenly ciliated. The ducts from the liver open in the dorsal end of this portion of the stomach. The epithelial cells of the ventral portion of the stomach are short, stain deeply, and carry a quantity of short cilia. Leaving the ventral end of the stomach, the intestine bends dorsally, and follows the posterior walls of the stomach nearly to its dorsal end. Here the loops already described are formed. From the loops the intestine passes posteriorly ventral to the heart, bends around the posterior side of the posterior adductor muscle, and opens into the mantle chamber. It is composed of short ciliated cells that stain deeply. Its lumen varies greatly in size, according to the amount of matter it contains.

LABIAL PALPS.

Soon after the embryo acquires its second gill lobe the epithelium around the mouth, and for a short distance along the sides of the body, becomes ciliated (fig. 41). This ciliation precedes the formation of the palps, and, to a certain extent, marks out the region where they will form. The cilia are more numerous immediately anterior to the mouth than they are immediately posterior to it, and they soon extend along the sides of the body for about half the width of the foot. The position of the ciliated patches on the body-wall is such that the dorsal portion of each tends to lie horizontally, and the ventral portion tends to the vertical position (fig. 62, *lp.*). The groove thus formed becomes the groove between the outer and the inner palps. The portion above the groove forms the outer palp, and that below the groove the inner palp. This is accomplished by the growth and folding of the body-wall. The outer palp begins to grow first, and in such a way that the line marking the dorsal limit of the cilia becomes the free margin of the palp. This leaves the inner surface of each outer palp covered with cilia, and the outer surface unciliated. The two outer palps are continuous anterior to the mouth, where they form a slight ridge (figs. 54 and 63).

For some time after the outer palps form folds, the inner palps are represented by ciliated ridges (fig. 54), that reach some distance beyond the posterior ends of the outer palps. These ridges grow so that the lines marking the ventral limit of the cilia become the free margins of the inner palps. The two inner palps are continuous posterior to the mouth, where they form a slight ridge (figs. 55 and 63). Like the elevation anterior to the mouth, this never becomes prominent.

The inner surface of each outer palp becomes folded near its anterior end to form ridges and grooves (fig. 55), and the postero-ventral portion protrudes to form a lobe. This lobe is the beginning of the formation of the palp appendage. The edges of this lobe soon begin to thicken, and a groove is left between the ridges thus formed. This is accompanied by a considerable growth in length (fig. 56, *pap.*). At this stage of development the palp appendage is seen to correspond to two of the ridges on the general surface of the palp, with a groove enclosed between them.

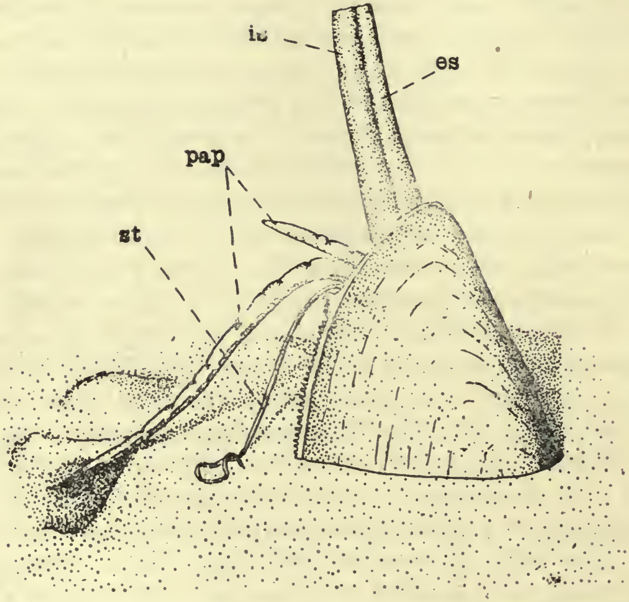
Posterior and dorsal to this appendage another smaller appendage is formed (fig. 56). This is also on the outer palp, and consists of two ridges with a groove between them. It never grows to be very long, but resembles the large appendage that lies ventral to it in its formation.

As development proceeds the larger appendage (fig. 56, *pap.*) twists, so that its groove opens dorsally and posteriorly (fig. 57, *pap.*), and the smaller appendage twists so that its groove opens ventrally. This double twisting brings that portion of the small appendage that was dorsal nearly or quite in contact with that portion of the large appendage that was ventral, so that for a short distance the two grooves together form a canal that opens anteriorly between the two palps (fig. 57). During the development of the palp appendages both outer and inner palps have grown to be quite large, and their ciliated surfaces have been thrown into series of ridges and grooves.

The palps on each side of an adult animal consist of two large, somewhat triangular folds of tissue (fig. 48, *lp.*), united to each other along their dorsal margins, and suspended from the body-wall by a thin membrane. The outer palps on the two sides of the body are connected in front of the mouth by a small ridge that occupies the position of an upper lip. In the same way the inner palps are connected by a ridge posterior to the mouth that is comparable to a lower lip. The corners of the mouth are continuous with the space between the two palps of each side. The opposed surfaces of the palps are densely ciliated, and thrown into a series of ridges and grooves that tend to lie opposite each other on the two palps. Near the free margins this arrangement may be considerably broken. Large blood-spaces follow along these ridges. Each outer palp is supplied with two grooved appendages that originate near its dorsal margin. The most ventral of these appendages (fig. 48, *pap.*) can be extended far beyond the margin of the shell, and is used to elevate mud with the contained food. The dorsal appendage sets over the anterior end of the groove of the ventral appendage, and with it forms a short canal that opens between the palps. Each ventral palp appendage is supplied with longitudinal muscles (fig. 66, *lm.*), that are continued in from the body-wall; with a large nerve (*pn.*) that originates in a cerebral ganglion, and runs posteriorly along the united dorsal margins of the outer and inner palps; and with a continuous blood-space (*bs.*). The epithelium lining the groove of the appendage is very thick, and is densely covered with cilia. The nuclei of these epithelial cells are very long and slender. The muscles in the palp appendages are so placed that their contraction causes the appendages to curl, as shown in fig. 48, *pap.*

It is not easy to observe individuals of this species while they are feeding, as they normally live entirely covered by the mud. If specimens are placed in a dish of sea water, in which there is only a thin layer of mud, the action of the palp appendages may be observed. It is well to use as much mud as possible without affording the animals an opportunity to bury themselves, and to use specimens that have not been in mud for several days and are accordingly hungry. The mud is passed along the grooves of the palp appendages by the action of the cilia, and finally conducted between the palps, where tne cilia carry it to the mouth. Very few specimens have shells that are transparent enough to allow observation of processes carried on inside of the shell, but there can be no doubt as to the path taken by the mud after it has started up the grooves in the palp appendages.

Feeding is much more easily observed in the case of Yoldia limatula. In this species the animal has frequently as much as one-third of the posterior end of the shell above the mud while feeding (text-fig. T). The palp appendages are protruded, and one at least bends over and inserts its tip in the mud. By the action of the cilia in the longitudinal groove, large quantities of mud and food are elevated. There is no reason to suppose that the palp appendages of Nucula are not as effective as those of



Text-fig. T.—An adult specimen of Yoldia limatula as it appears while feeding. *es*. Exhalant siphon. *is*. Inhalant siphon. *pap*. Palp appendages. *st*. Siphonal tentacle.

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Yoldia, but the method of life makes observation more difficult. As suggested by Mitsukuri (11), it seems probable that the large palps with their numerous large blood-spaces may be important respiratory organs.

GILLS.

A short time after the embryo sheds its test, a portion of each lobe of the mantle near its posterior border begins to thicken (fig. 39, *g.*) and then to project anteriorly. These thickenings are the beginnings of the gills. They grow rapidly, acquire cilia, broaden dorso-ventrally, and each begins to divide into two lobes (fig. 40, *g.*). The formation of the lobes is due to unequal growth more than to constriction. Each lobe is at first a little knob that is flattened slightly laterally. As growth proceeds the ventral lobe broadens and flattens along its anterior border preparatory to the formation of another lobe. Coincident with these changes in the ventral lobe, the dorsal lobe grows anteriorly, and forms a rather long finger-like process or filament, that closely resembles the filaments of the developing gills of other Lamellibranchs (fig. 41, *g.*). New lobes are added to the gill by the unequal growth and division of each ventral lobe in its turn, and as the new lobes are formed the more dorsal lobes lengthen.

Throughout life the gill occupies a decidedly dorso-ventral position, but growth carries the ventral end some distance toward the posterior end of the animal, so that the adult gill lies somewhat diagonally (fig. 48, *g.*). In Yoldia (text-fig. L) the gills lie more nearly parallel to the long axis of the body.

The chitinous support of the gill makes its appearance when the gill is still in the two-lobed condition. At first it consists of a thin plate lying just beneath the epithelium on the anterior border of the gill, and is continued from one lobe into the other. Its ends lie near the anterior extremity of each lobe. As the ventral lobe flattens the chitinous plate is extended along its anterior border, so that with the formation of the third lobe the plate is extended into it. In this way, as new lobes are formed, the chitinous plate is extended into each, and continues to be connected throughout the length of the gill. As the lobes grow to form filaments, the chitinous plates extend with them, and each becomes trough-shaped with the open side of the trough directed away from the corresponding lobe of the mantle. Later the free edges of the trough are brought near together, and the support in each filament practically assumes the form of a tube that extends out nearly to the tip of each filament. The tubes that support the different filaments are united at their bases, so the chitinous support is continuous throughout the gill.

As the lobes elongate to form filaments, the cilia on each becomes restricted, so that the side that is turned away from the lobe of the mantle to which it is attached becomes quite free from them. On the remaining sides the cilia are long and powerful.

About the time that the fourth division of the gill is formed the mantle begins to thicken at the bases of the filaments, between them and the shell (fig. 45). These thickenings are generally opposite the bases of the filaments, and connected with them, but as there are sometimes more plates on one side of the gill[1] of the adult animal than on the other, the thickenings are probably not always formed in this position.

They represent the beginnings of the outer plates of the gill. The filaments, at the bases of which these thickenings are formed, form the inner plates of the gill.

For a considerable time the outer plates remain much smaller than the inner plates, and they never quite equal them in size (fig. 53). As the outer plates of the gill are formed, the chitinous support is carried out into them as branches from the portion that runs lengthwise of the gill. These branches become trough-shaped, with the open part of the trough directed away from the inner plates. Finally, the free edges of the troughs come close together, as described in connection with the other set of filaments or plates.

The chitinous material at the bases of the two sets of plates also become trough-shaped, and has the open portion of the trough directed away from the plates. Thus the chitinous support of the gill consists of two series of troughs, bent so as to form tubes, each of which is connected by one end to the side of a larger trough that runs lengthwise of the gill. The whole might be compared to a large trough with a series of spouts leaving each side, the individual spouts of the two series being placed opposite each other. Later, bridges are built across the main trough in the intervals between the side spouts. The whole system is in direct communication with the blood-spaces of the gill, but probably is not concerned with the circulation of the blood.

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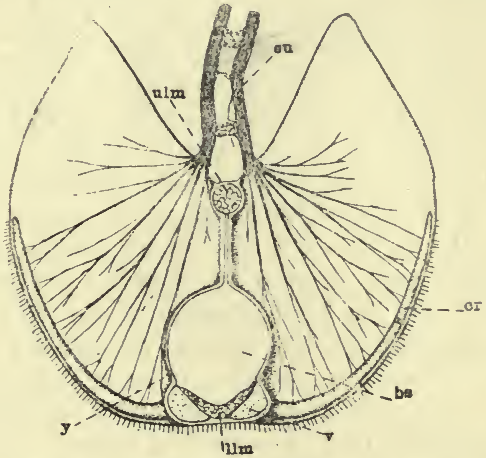
[1] The term gill is for convenience applied to the respiratory organ on one side of the animal, although writers agree that it probably corresponds to the two gills found on each side of most Lamellibranchs.

The two sets of plates do not lie parallel to each other, but they grow away from each other at an obtuse angle. The inner plates grow almost in an anterior direction, and the outer plates grow laterally and a little posteriorly, so that the angle formed by the two sets of plates on the two sides of the gill is visible when the animal is viewed from the side. The suspensory membrane, formed by the growth of the mantle at the base of each gill, makes it possible for the gill to take up this position.

The filaments begin to grow into flattened triangular plates about the time that the fourth division of the gill is formed. This is accomplished by slow, unequal growth, and throws no light on the phylogeny of the gill. It seems to be a matter of individual opinion whether each of the plates should be considered to be homologous with a descending filament of an ordinary Lamellibranch gill, or whether it should be considered to be homologous with both a descending and an ascending filament.

The adult structure of the gill of Nucula has been so carefully and accurately described by others, that were it not for the sake of completeness, it would not be necessary to describe it here. Mitsukuri's (11) description of the gill of Nucula proxima holds good in all essentials for the gill of this species, and since his description was published others have verified and supplemented his results (7, 13, and 16) until our knowledge of the structure is comparatively complete.

The adult gill of Nucula delphinodonta is suspended from the body-wall by a fold of tissue, the suspensory membrane (fig. 53, *gs.*), that was originally a fold on the inner surface of the mantle lobe. The suspensory membrane contains between its walls a large blood-space that communicates near its anterior end with an auricle of the heart, and throughout its length communicates with blood-spaces in the mantle. At intervals it communicates with similar spaces in the body proper. Unlike the suspensory membrane of Yoldia (text-fig. U), this membrane is not very muscular, but some muscle-fibres are always present. The epithelium covering the outer surfaces of the suspensory membranes, those surfaces that are turned away from the mid-line of the body, is modified to form a portion of the hypobranchial glands.



Text-fig. U.—A pair of plates from a gill of Yoldia limatula. *bs.* Blood-space. *cr.* Chitinous rod. *llm.* Lower longitudinal muscle. *su.* Suspensory membrane. *ulm.* Upper longitudinal muscle. *v.* Cut surface of a chitinous rod. *y.* Cut wall of the gill plate where it bends to join the plate anterior to it.

Each suspensory membrane bears two series of gill plates that generally lie opposite each other. Occasionally a gill occurs in which there are more plates on one side than on the other, but even in these cases the order is interrupted only for a short distance. The number of plates differs with the size of the individual, but about twenty pairs seem to be common for well-grown specimens. Each plate is thin and triangular, and is composed of epithelial walls, between which there are loose connective tissue, large blood-spaces, and the chitinous framework. The epithelial walls on the edges of the plates that are directed away from the suspensory membranes are thickened and covered with strong cilia. This thickened ciliated epithelium extends between the plates for a short distance, but most of the epithelium is quite thin and destitute of cilia. The wall of each plate is continuous with the wall of the plate that lies in front of it, with the wall of the plate that lies behind it, and with the plate on the other side of the gill that lies opposite to it. Near the border furthest from the suspensory membrane, the opposing walls of the two series of gill plates are separated so as to form a large blood-space (fig. 53, *bs.*), that runs the whole length of the gill. This space is continued as a narrow slit to the base of the suspensory membrane. Thus the blood-space in the suspensory membrane is in direct communication with the blood-space of each plate, and in the gill the blood is free to flow from one part to another.

The chitinous framework consists of a bridged trough that occupies the bottom and part of the sides of the blood-space that lies between the two series of plates, and of two series of side spouts that project into the plates on the two sides, and lie in contact with the thickened epithelium. Although the chitinous framework is arranged as a system of troughs and spouts that, from their position, must be filled with blood, they are probably not directly concerned in the circulation of the blood.

Between the chitinous trough and the suspensory membrane there is a small bundle of muscle-fibres that is continued the whole length of the gill (fig. 53, *lm.*). This bundle lies in the open part of the chitinous trough, and probably corresponds to the large bundle that occupies a similar position in the gill of Yoldia (text-fig. U, *llm.*). A second longitudinal bundle of muscles is found in the gill of Yoldia (*ulm.*), but this does not seem to be present in this species. A few of the muscle-fibres in the suspensory membrane seem to be continued into the plates. They are not numerous, and they have not been carefully followed. The gill of this species is so small that it is not favourable for the determination of minute details.

The gills probably act as respiratory organs, but their small size, together with the blood-supply of other parts, makes it seem probable that other organs, such as the mantle and the palps, are also concerned in respiration. The opaque character of the shells of adult animals makes it quite impossible to observe the normal movements of the gills. They can be seen to move slightly, however, and it seems probable that the suspensory membranes contract slightly at intervals. Such movements would be useful in causing movements in the contained blood, but they are not sufficient to cause strong currents of water. The shape of the gills is not such as would make them efficient pumping organs. (Compare fig. 53 and text-fig U.) Inasmuch as these animals live entirely covered by mud, the production of strong currents of water could not be beneficial. As the animal wanders around in the mud the fæces naturally drop out of the open mantle chamber.

It would be a matter of some interest if the exact relationship of the gills of Nucula and Yoldia could be determined. It would seem to be a comparatively easy task to account for the changes in the shape and structure of the gill of Yoldia if we were to start with a gill such as has been described for Nucula. The habits of Yoldia are such as to render the formation of strong currents of water absolutely necessary, for otherwise the mantle chamber would become clogged with fæces and dirt. The gill of Yoldia might have been perfected for pumping water from a Nucula-like gill. It would, however, be equally easy to account for the reverse modifications when we consider what the formation of strong currents of water by an animal entirely covered by a soft, slimy mud would mean. If we follow the generally accepted theory of the gill, the former change would seem more likely than the latter, though it is quite possible that nothing like a direct change from one to the other has taken place. The generally accepted theory of the gill has grown up as the result of structural and embryological considerations, and but scant attention has been given to probable modifications for the special purposes of the animals. Until we have much more detailed knowledge regarding the habits of most of the Lamellibranchs that have plate gills, and of some of the supposed near relatives of these Lamellibranchs, it seems to me that we lack the necessary data to give the derivation of the gill with anything like accuracy. There is much in the structure and embryology of Nucula that points to a generalised type, and in this much it seems natural to look at the gills as primitive; but the gills of Yoldia—its undoubted near relative—are so remarkably well adapted for the performance of a special function, that it hardly seems safe to regard them as slightly modified gills until there are more careful observations on the habits of the other forms.

I recognise fully the mass of evidence in favor of the primitive form of the plate-like gill. My only plea is for caution.

HYPOBRANCHIAL GLANDS.

The epithelium on the inside of the posterior end of each lobe of the mantle, and on the outer side of a corresponding portion of the suspensory membrane of each gill, is glandular, and has been termed the hypobranchial gland. When these glands are present in Lamellibranchs, their secretions seem to correspond very closely to mucus, and they are generally referred to as mucous glands. During the greater part of the year the hypobranchial glands of both sexes of Nucula delphinodonta are rather small and inconspicuous. They contain rounded or oblong masses of a refractive material that takes no stain. The cells themselves are small, and do not seem to be secreting actively. The hypobranchial glands of specimens of males seem to have the appearance that has been described, no matter what time of the year they are collected. As the breeding season approaches, the hypobranchial glands of the females become greatly distended with secretions. The rounded or oblong masses that are common at other seasons of the year are now seldom found, and the cells are packed full of rather large granules. Immediately after the brood-sac is formed, the cells of the hypobranchial glands appear shrunken and free from granules, and the glands have the appearance of having discharged their secretions. After examining a large number of specimens, I have become convinced that the hypobranchial glands furnish nearly all of the material from which the brood-sacs are formed. Specimens kept in aquaria do not form brood-sacs, and accordingly the processes of their formation have not been observed, but it seems probable that the secretions from the glands are passed posteriorly by cilia on the mantle, and probably swelled out into a bubble by the respiratory current of water. While the material is still soft it adheres to the foreign bodies with which it comes in contact.

Well developed hypobranchial glands are present in only a limited number of Lamellibranchs, and their special function is hard to determine. It is interesting to find that they are concerned in the formation of the brood-sacs in this species, but this is the first instance that has been reported where such a sac is formed. It may be that other forms that possess especially large hypobranchial glands will be found to form similar brood-sacs, but this will not hold true for all. Nucula proxima has rather large hypobranchial glands, and I find that it does not form brood-sacs. Such a case as this, where it is known that brood-sacs are not formed, seems to indicate either that the glands have some function to perform other than providing the material for the formation of brood-sacs, and that Nucula delphinodonta has adapted them to this purpose; that they are retained from forms that originally formed brood-sacs, in which case we must suppose that the ancestors of all forms that possess hypobranchial glands formed brood-sacs; or that in forms where brood-sacs are not formed the glands are, when present, mere vestiges, and are not now functional.

The latter explanation seems unlikely, as the glands of Nucula proxima are better developed than vestiges are likely to be. If the second explanation is accepted, we must regard the rearing of embryos in brood-sacs as more primitive, for this group at least, than throwing the eggs in the water where the embryos have to take care of themselves. From the standpoint of specialisation this seems to be very unlikely, and the fact that the embryos of Nucula delphinodonta possess tests that seem to serve no purpose, while similar tests function as organs for locomotion in other forms, points clearly to a condition when all of these embryos depended on their own activities for protection. It seems most likely that Nucula delphinodonta has made use of already existing glands to furnish the secretions for the formation of its brood-sacs, and that they may have other functions to perform.

PERICARDIUM.

A short time before the shell-gland begins to fold at the sides to form the lobes of the mantle, a space appears between the stomodæum and the gut, and a little later a space begins to form between the shell-gland and the gut (fig. 24). These two spaces are separated by the gut, but in preserved material they are frequently connected around the sides of the gut. While these connections may be due to shrinkage caused by the treatment with preservatives, it seems more likely that the spaces are normally connected with each other. It is just possible that these spaces may be traced back in their formation to the blastocœle, but it is more probable that the blastocœle entirely disappears, and that they represent a schizocœle. At first the space ventral to the gut is larger than that dorsal to it, but the latter grows as the mantle arches dorsally, and the ventral space remains practically unchanged.

As the foot begins to take form the ventral space becomes quite small, and about the same time that the embryo sheds its test it disappears altogether. A short time before the test is shed the dorsal space reaches its greatest size (figs. 25 and 26). About the time that the test cells begin to break apart, the stomach is carried dorsally some distance into this space (fig. 34). Two fibres, that in shape suggest muscle-fibres, extend from the anterior end of the stomach to the mantle. Their position suggests that they may aid in moving the stomach dorsally, but of this I have no proof. As the stomach moves dorsally they become shorter and thicker, but there is no evidence that they are moving factors. Until casting is completed, the apical plate and the stomodæum lie between the edges of the shell-valves, and keep them from being closed. When they are removed, the contraction of the adductor muscle closes the shell, and the body, which has until now been lying between gaping valves, is made to change its shape and position. The stomach and liver pouches are forced into the dorsal space until the dorsal end of the stomach comes in contact with the mantle.

This divides the space into anterior and posterior parts (fig. 35). There is no longer room for the liver pouches to retain their form and position, and as the body continues to move dorsally they are flattened out and soon go to pieces (fig. 36). Most of the cells that formerly composed their walls become scattered and rounded, and the anterior space becomes entirely filled (fig. 39). The posterior space, somewhat diminished in size, persists, and finally becomes the pericardium (figs. 40 and 41). The pericardial space is not smooth as it has been necessary to represent it in the figures. Mesoderm cells project into it from the surrounding tissue, and others lie comparatively free within it. As yet it lies almost wholly dorsal to the intestine, but just before the heart is formed it is extended beneath the intestine, and begins to have a rather definite epithelial lining. The epithelial lining seems to be formed by the change in shape and position of cells in the immediate vicinity. I find no indication that the pericardium originates as a pair of pouches, as has been described by Ziegler for Cyclas cornea (20).

VASCULAR SYSTEM.

Small connected cavities are present throughout the body from an early time, but a true vascular system, with a heart and anything like a definite circulation, is not to be distinguished until much later, and a closed system of vessels with capillaries is never present.

The heart is formed about the time that the gill becomes well divided into two lobes, or just before the third lobe is formed. It seems to be formed by the hollowing out of a strand of mesoderm that stretches across the pericardial cavity. I have seen nothing that would indicate that the heart has a double origin, as Ziegler has described for Cyclas cornea (20). Mesoderm cells in the pericardial cavity and along its walls arrange themselves to form a strand that becomes hollow and begins to pulsate. From the first appearance of its cavity the heart surrounds the intestine (figs. 41 and 67). Most specimens show the heart collapsed with its walls in contact with the intestine, but some specimens have it distended with blood. In all cases it is easy to determine that the heart is perforated by the intestine, but it is especially evident in specimens where the heart is distended. In most of these cases the intestine lies nearer the ventral than the dorsal wall of the heart, and in many cases it lies directly in contact with this wall. At this stage the heart is not separated into auricles and ventricle (fig. 67, *h.*). It is in the form of a bent spindle, the two ends of which communicate with the blood-spaces of the gill. The larger median portion arches dorsally and surrounds the intestine. Anterior and posterior aortæ leave the heart, but no attempt has been made to follow them, until the adult stage is reached.

For a considerable time after its formation there is no appreciable change in the heart. About the time that the eighth pair of gill plates are formed it begins to be separated into ventricles and auricles. The auricles are at first very small and narrow. They extend only a short distance from each gill, and are separated from the ventricle by slight constrictions. There has been no change in the relative positions of the heart and intestine. At a slightly later stage, when the gill has about ten pairs of plates, the ventricle of the heart begins to change its shape. This seems to be due to the growth of the kidneys, which push anteriorly ventral to the pericardium. As the kidneys grow, the two sides of the heart are pushed dorsally, while the middle part of its ventral wall is held in its original position by the intestine. In this way the ventral wall is pulled out into a sort of trough in which the intestine lies (fig. 68, *h.*). Continued growth deepens the trough until it is considerably deeper than the intestine is wide. The heart gradually closes in, dorsal to the intestine, at the anterior and posterior ends of the trough, until it becomes free from the intestine, and lies dorsal to it (fig. 69). This is a very slow process, and is not completed until after the animal has reached sexual maturity.[1]

The adult heart consists of a ventricle and a pair of auricles, separated from each other by constrictions that are much deeper on the dorsal than on the ventral surface (fig. 69, *h.*). The openings between the auricles and the ventricle are so small that they must be quite obliterated during contraction. A band of muscle occurs near the end of each auricle, that keeps the blood from flowing back into the spaces of the gills. Each auricle is somewhat conical, small where it joins the gill, and considerably enlarged at the end next to the ventricle. The ventricle is swollen next to the auricles, and flattened over the intestine. The swollen ends of the auricles and the corresponding swellings the ventricle make right and left enlargements that superficially might be mistaken for two hearts.

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[1] Every specimen of Nucula proxima that I have examined has its heart perforated by the intestine. The specimens are all of good size, and many of them are the same ones from which I obtained eggs and sperm.

A blood-vessel leaves the anterior end of the ventricle on the left side of the intestine, and not in contact with it. Another blood-vessel leaves the posterior end of the ventricle above the intestine and in contact with it. The anterior vessel is somewhat larger than the other. It runs forward over the dorsal end of the stomach and sends branches to the liver and genital organs, to the stomach and loops of the intestine, to the foot, to the labial palps, and to the anterior portions of the lobes of the mantle. The vessel that leaves the ventricle posteriorly is at first dorsal to the intestine, but it soon becomes ventral to it, and is distributed to the posterior part of the body.

All of the blood-channels seem to end in rather large connected spaces, that ramify throughout the body. The course of the blood cannot be traced in these spaces. The blood-spaces of the foot, beside providing for the ordinary blood-supply, serve as reservoirs in which blood can be forced to extend the foot. By suppressing some channels and squeezing blood into others different results may be obtained. Blood must undergo respiratory changes in the gills, the mantle lobes, and the palps.

The opinions of writers on Lamellibranch morphology, regarding the primitive form and position of the heart, are very different. Milne-Edwards (10) thought that the double appearance of the heart of Nucula and Arca pointed toward a primitive condition in which the heart was double. Thiele (19), basing his conclusions on Ziegler's observations on the formation of the heart of Cyclas, holds that the heart was probably originally a double organ, and that upon uniting in the median line it has taken up the various positions in regard to the intestine. Grobben (5) considers the single heart primitive, and thinks that the double condition is the result of changes in the position of retractor muscles. Pelseneer (13) and others, depending largely upon the position of the heart in Nucula and Arca, have considered the dorsal position of the heart to be the primitive position. Stempell (17) rightly holds that the ventral position of the heart of Malletia chilensis destroys the foundation of Pelseneer's reasoning, inasmuch as Nucula and Malletia are closely related forms. Stempell apparently considers the perforated heart to be the most primitive. From this position the heart may become dorsal or ventral to the intestine by a comparatively simple process.

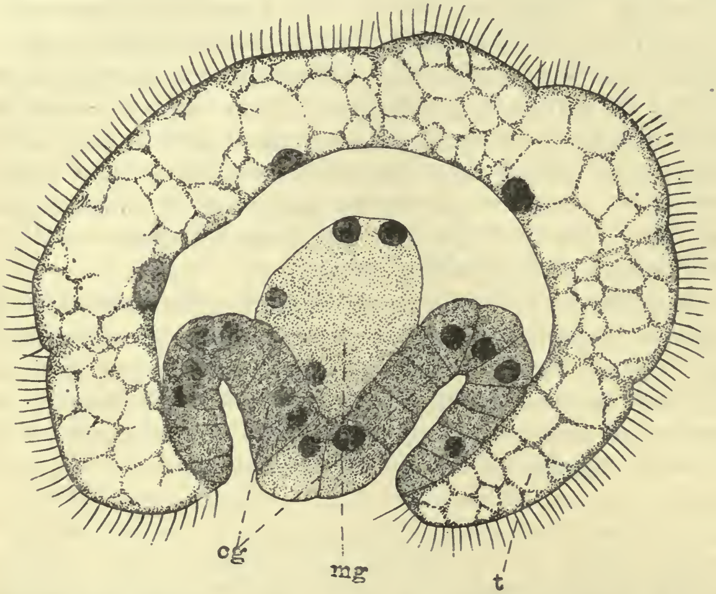
The development of the heart of Nucula seems to indicate that the perforated heart is more primitive than the dorsal heart in this group. While, as Stempell holds, it seems most reasonable to consider a perforated heart that may become either dorsal or ventral by comparatively simple changes as more primitive than either a dorsally or a ventrally placed heart—where, in order to reach the opposite extreme, the heart would have to enclose the intestine, and then become free on the other side,—there is still nothing to prove that the ventral position of the heart is not primitive. The development of the heart of Malletia would accordingly be of considerable interest.

As neither the pericardium nor the heart of this Lamellibranch seems to be formed as a paired structure, there is nothing here to further the view of Thiele (19) that the position of the heart in regard to the intestine depends simply upon the position of two lateral hearts, that may, as a matter of convenience, fuse dorsally, ventrally, or around the intestine.

NERVOUS SYSTEM.

The cerebral ganglia are formed in direct contact with the apical plate. The cells from which they originate can first be distinguished as a group soon after the surface cells that form the test become ciliated (fig. 15, *cg.*). They frequently remain as surface cells for some time, and they doubtless originate as surface cells in all cases. The group of cells is not distinctly paired, and does not invaginate as it does in Yoldia. Each cell becomes much larger at the inner end than at the end that comes to the surface. Although a test cell lies between the cerebral ganglia and the apical plate they still remain in contact beneath this cell. Little change occurs in the appearance, size, or position of the cerebral ganglia until the test is cast away, and until then no other part of the nervous system can be distinguished.

When the test-cells break apart and accumulate near the anterior end of the embryo (fig. 34) a portion of the body of the embryo is carried dorsally at the expense of the large dorsal space. This dorsal movement includes the cerebral ganglia (*cg.*). When casting is completed, and the valves of the shell are closed, a further dorsal movement occurs, that results in the filling of the greater part of the dorsal space. This movement places the cerebral ganglia in position posterior to the anterior adductor muscle (figs. 35 and 36, *cg.*). The foot now begins to grow quite rapidly, and the pedal and visceral ganglia begin to form (fig. 36, *pg.* and *vg.*). Both pairs of these ganglia are formed as thickenings of the surface ectoderm. The thickenings that give rise to the pedal ganglia begin to form first, but both pairs of ganglia are in process of formation at the same time. Owing to the character of the embryonic tissue it is very difficult to determine how the commissures that connect the ganglia arise. They are first found very close to the surface, almost, if not quite, in contact with the ectoderm. Later they sink deeper into the body. The cerebro-visceral commissures are quite thick, and differ from the cerebro-pedal commissures in



TEXT-FIG. V.—Transverse section of a forty-five hour embryo of Yoldia limatula, taken through the cerebral pouches. *cg.* Cerebral pouches. *mg.* Anterior wall of the mid-gut. *t.* Test.

having much the same structure as the ganglia themselves. In the earlier stages I have been able to demonstrate only a single cerebral origin for each cerebro-pedal commissure. This may be due to the difficulty of tracing commissures in embryonic tissue. Later stages show two separate origins very distinctly.

The double origin of the cerebro-pedal commissures has been regarded by Pelseneer (13) as an indication of the presence of cerebral and pleural ganglia in each anterior nerve-mass. Furthermore, Pelseneer and others find that each mass is divided by a constriction into two rather distinct parts. I have not been able to satisfy myself that there is a distinct separation into cerebral and pleural ganglia, either in this or the other forms that I have studied.

The cerebral and pedal ganglia are about equal in size, but they differ in shape (fig. 48). The visceral ganglia are smaller than the cerebral ganglia, but compare pretty well with them in shape. Each cerebral ganglion is large at its anterior end, and tapers posteriorly into the cerebro-visceral commissure. The commissure that connects the two cerebral ganglia is a broad, somewhat flattened band, that passes between the œsophagus and the anterior adductor muscle, and joins their anterior ends. The cerebral ganglia give rise to a number of nerves. A large nerve leaves the ventral side of each near its anterior end, passes ventrally along the posterior and ventral surfaces of the anterior adductor muscle, to which it sends branches, and is distributed to the anterior and ventral portions of the corresponding lobe of the mantle. Just posterior to the origin of the pallial nerve, and a little closer to the median line, another nerve, about equal to the pallial nerve in size, leaves each cerebral ganglion. This nerve follows along the fold of the tissue that suspends the labial palps and is continued into the palp appendage. Other nerves from these ganglia are distributed to the visceral mass and to the dorsal portions of the foot muscles. Posterior and still further toward the median line than the palp nerve, the two portions of each cerebro-pedal commissure leave each cerebral ganglion, one a little anterior and ventral to the other. The two portions run posteriorly a short distance, and join to form a single commissure that is continued to the pedal ganglion of the same side. A nerve leaves each cerebro-pedal commissure dorsal to the corresponding otocyst, and is continued to it. This nerve is generally supposed to have its origin in the cerebral ganglion, and the angle at which it issues from the commissure indicates that this is probably the case. The otocystic nerve is about equal in size to the posterior division of the cerebro-pedal commissure. Stempell (18) finds that each otocystic nerve of Solemya togata leaves the cerebral ganglion direct, and runs an independent course to the otocyst. He also finds that each cerebro-pedal commissure leaves the cerebral ganglion as a single strand. He thinks that this is a double commissure, because it receives fibres from what he considers cerebral and pleural ganglia.

It seems more likely to me that the nervous systems of all Mollusca have been derived from some such a generalized type as is found in Chiton, and that each class has developed ganglia according to its needs, than that the ancestors of Lamellibranchs possessed the comparatively complex system of ganglia found in Gastropods. If this is true, it is easy to understand why Gastropods with their complicated head apparatus should develop ganglia for which Lamellibranchs have no need. Accordingly the necessity to homologize all of the ganglia in the two classes disappears.

In most Lamellibranchs the otocystic nerves spring from the cerebro-pedal commissures, and they are supposed to originate in the cerebral ganglia. In Solemya togata, Stempell finds that the otocystic nerves leave the cerebral ganglia direct, and are not included in the cerebro-pedal commissures in any part of their length. Is it not possible that the posterior root of the cerebro-pedal commissure, in forms where there are two roots, is the central end of the otocystic nerve?

The pedal ganglia (fig. 48, *pg.*) are rounded and nearly equal to the cerebral ganglia in size. They lie close together, and they are connected by a moderately large commissure. The nerves from the pedal ganglia supply the muscles of the foot. They need no special mention.

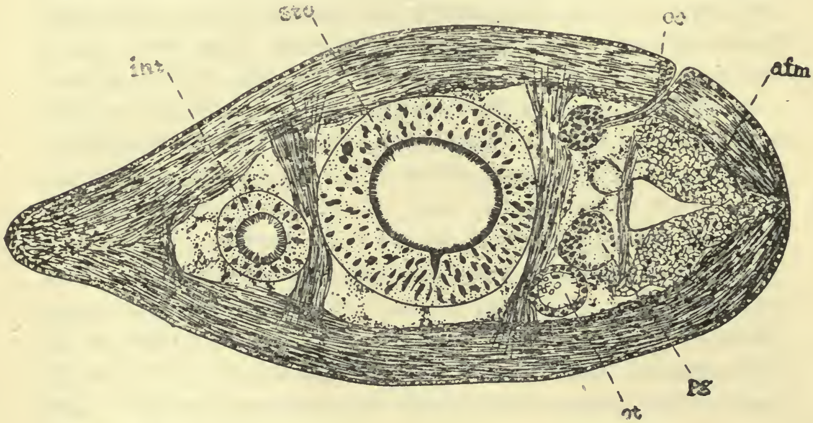
The visceral ganglia (fig. 48, *vg.*) are the smallest of the three pairs of ganglia. In shape they resemble the cerebral ganglia, but they are turned in the opposite direction. Each visceral ganglion is elongated, and gradually tapers anteriorly into the cerebro-visceral commissure. The two ganglia lie far apart, and are connected near their posterior ends by a long and rather thick commissure. A rather large nerve leaves the posterior end of each ganglion, runs posteriorly ventral to the posterior adductor muscle, and, besides giving branches to this muscle, supplies the posterior and ventral portions of the corresponding lobe of the mantle. Anterior and ventral to the posterior pallial nerves another rather large nerve leaves each ganglion. This nerve runs along the inner side of the suspensory membrane of the corresponding gill nearly to its posterior end.

OTOCYSTS.

The otocysts are formed soon after the embryo sheds its test. They originate as invaginations in the body-wall, a little posterior and dorsal to the pedal ganglia. The invaginations deepen and close over to form what seem to be closed sacs, that soon come to lie near the pedal ganglia in the interior of the foot. As in the case of Yoldia, these sacs are apparently entirely closed. Soon after the otocysts are formed, before the gills acquire their second lobes, otoliths appear. The otoliths have the appearance of little crystalline fragments, but I am inclined to think that they are formed in the otocysts, and are not introduced through the otocystic canals, as has been held by some writers. The particles seem to be too large to have been introduced through canals that, at this stage, I am unable to find. Again, the otocysts never seem to contain diatoms. Diatoms are very abundant in the brood-sacs in which the embryos are carried, and form a large part of the animal's food. Many of them are well shaped to pass through small openings, and one would expect to find them occasionally in the otocysts, if the contained material consists of foreign bodies that have gained access through the otocystic canals.

About the time that the gills acquire their sixth pair of plates the otocysts can be seen to be connected with the surface of the foot (figs. 46 and 64,*ot.*). At first the connection seems to be solid, but a little later openings can be traced from the otocysts to the exterior. These tubes, the otocystic canals, are quite slender near the otocysts, but widen toward the surface of the foot. From each otocyst the canal passes anteriorly, laterally, and a little dorsally to open to the exterior (figs. 46 and 64,*ot.*).

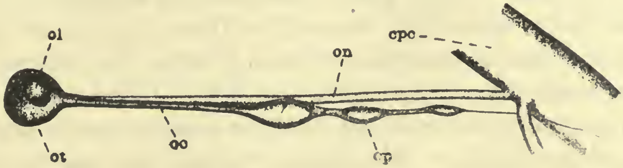
The position of the external opening is not just what might be expected if the otocystic canals are remnants of the invaginations that formed the otocysts. The otocysts are formed just posterior and a little dorsal to the pedal ganglia. As they develop, they sink into the interior of the foot and become permanently settled near the ganglia at points nearly opposite their points of origin. As the same relation between organs in his region is retained during the whole of the development, there is no reason to think that growth is more from one side than from another. If, then, the otocystic canals are remnants of the original invaginations, we might expect them to run almost perpendicular to the surface instead of opening so far anterior and dorsal. It might be thought that the development of the anterior foot muscles has crowded the stomach, ganglia, and otocysts posteriorly, and caused the otocystic canals to take up this position, but reference to fig. 64 will show that before these muscles become very large the otocystic canals open further toward the anterior than when these muscles become highly developed (text-fig. W). This seems to show that the muscles, as they develop, project anteriorly, and do not affect the organs lying behind them.



Text-fig. W.—Horizontal section of the foot of an adult Nucula delphinodonta. The otocystic canals leave the dorsal side of the otocysts, so that in this section only the dorsal wall of the otocyst is seen on the side where the canal is present. *afm.* Anterior foot muscle. *int.* Intestine. *oc.* Otocystic canal. *ot.* Otocyst. *pg.* Pedal ganglion. *sto.* stomach.

In a former publication (1) I have described the imperfect otocystic canals of Yoldia limatula. The canals are short and do not reach the surface of the foot. Frequently a number of closed pouches are connected with the end of each otocystic canal by a strand of fibrous material (text-fig. X). Stempell reports that the otocystic canals of Leda pella are very rudimentary. He has never been able to trace them with certainty to the surface skin (17). The conditions illustrated by these two forms can easily be explained as the result of degeneration, but there is no direct evidence that this is the case. If the canals are not remnants of the original invaginations, the imperfect canals may be structures that have never been perfect canals, or they may indicate the degeneration of canals that have at some time been perfect.

The nerve-supply of the otocysts has been discussed in connection with the nervous system. It seems possible that the dorsal roots of the cerebro-pedal commissures may be the central ends of the otocystic nerves.



Text-fig. X.—Otocyst of Yoldia limatula. *cpc.* Cerebro-pedal commissure. *oc.* Otocystic canal. *ol.* Otolith. *on.* Otocystic nerve. *op.* Otocystic pouch. *ot.* Otocyst.

MUSCULAR SYSTEM.

For convenience in treating the subject the muscles may be grouped into those concerned in shutting the shell, in moving the foot, in propelling blood, in retracting the margins of the mantle, in retracting the palp appendages, and in raising the gills. Beside these muscles, there are many scattered and interlacing fibres that are concerned in making many of the movements.

The anterior adductor muscle (figs. 25 and 36, *aa.*) is formed somewhat earlier than the posterior adductor muscle, and throughout life the former is larger than the latter (fig. 48). When the anterior adductor muscle is first formed (fig. 25, *aa.*), it occupies a position at the anterior end of the dorsal space, very near the apical plate. Soon after the test is shed, it becomes surrounded by tissue that is drawn up around it (figs. 35 and 39, *aa.*). The posterior adductor muscle is formed soon after the test is shed (fig. 39, *pa.*). It lies ventral to the intestine, and posterior to the visceral ganglia, and from its first appearance is surrounded by other tissue.

In the adult the adductors are attached to the shell, with their dorsal borders very near the ends of the rows of teeth. The function of these muscles is simply to close the shell. The contraction of the muscles, and the consequent closing of the shell, compresses an elastic pad known as the cartilage, that lies in the cartilage pit. As soon as the adductor muscles relax, the expansion of this piece of cartilage opens the shell. The epidermis is not thickened to form a prominent external ligament.

The foot is attached to the shell by three pairs of well developed foot muscles, and by a number of fibres that form a more or less connected series on each side, ventral to the genital organ and liver. Of the three pairs of foot muscles, one is posterior and two are anterior. The posterior muscles are inserted on the shell along the bases of the teeth, anterior and dorsal to the posterior adductor muscle. They extend anteriorly and ventrally along the sides of the foot, and form the strong retractors of the foot. The two pairs of anterior foot muscles are attached to the shell close together, along the bases of the teeth, posterior and dorsal to the anterior adductor muscle. In distribution, the anterior pair of these muscles corresponds to the two anterior pairs in Yoldia. They spread out along the sides of the foot, and are distributed to its posterior and ventral portions. The more posterior of the two pairs of muscles passes between the pair just mentioned, and is distributed to the anterior and ventral portions of the foot.

All of these muscles are closely bound together by their own fibres and by interlacing fibres, so that many movements occur that cannot be explained by direct pulls of one or more muscles. It should be remembered that the attachments of the fibres are all along the sides of the foot, and that many, if not most of the muscle-fibres, pull from one part of the body-wall to another, without changing the relation of the body to the shell. Thus the muscular side flaps of the foot can be spread apart after the animal has been removed from the shell.

Between the muscles, loose connective tissue and large blood-spaces occur. Many of the movements, especially those that result in the protrusion of the foot, seem to depend on the action of muscles on the fluids of the body, more especially upon the blood contained in the spaces of the foot. By obliterating some channels and forcing blood into others, different results may be obtained.

The muscle-fibres that are attached to the shell along the ventral border of the genital mass and liver are distributed to the body-wall. They are not as numerous as they are in Yoldia. I have found no indication of a special muscle at the posterior end of each series, as is the case with Yoldia (3).

The heart is largely made up of interlacing muscle-fibres. Each auricle is separated from the ventricle by a constriction (figs. 68 and 69, *h.*). It seems probable that, when the ventricle begins to contract, the contraction of the muscles in these constrictions closes the openings between the ventricle and the auricles so that the blood cannot flow back into them. Where the auricles join the blood-spaces of the gills and mantle lobes, the muscles probably act in the same way.

There are some muscle-fibres in the suspensory membranes of the gills that probably contract at intervals. The opaque shells make it impossible to watch the movements of the gills, but it will be seen that such movements as are made must force some of the blood out of the blood-spaces of the suspensory membranes. The movements are not enough to form strong currents of water, such as are formed by Yoldia (1).

The margins of the lobes of the mantles are never protruded far beyond the margins of the valves of the shell, and the pallial muscles are accordingly not excessively developed.

Each of the large palp appendages is supplied with a rather large muscle that is continued into it from the body-wall. It occupies the ventral (morphologically outer) side of the appendage (fig. 66, *lm.*), and is continued to its tip. This muscle serves to retract the appendage. Its position in the appendage is such that when the appendage is strongly retracted it is curled as shown in fig. 48. The muscle seems to be homologous with fibres that extend into the membrane that suspends the palps from the body-wall.

EXCRETORY ORGANS.

Just before embryos reach the stage where the second gill filaments begin to flatten, preparatory to forming the third gill filaments, a pair of narrow tubes appear just anterior to the visceral ganglia and ventral to the pericardium. The two tubes touch each other on the median line of the body, but their cavities do not seem to communicate. Laterally they are extended to the surface of the body, where they open into the mantle chamber. This is the earliest stage in which I have been able to distinguish the kidneys. I have not succeeded in determining whether the external openings are present from the beginning, or whether they are formed later. I am inclined toward the view that the kidneys are mesodermal in their origin; but this view is based simply on the length and narrowness of the tubes when they can first be distinguished. They may be formed as invaginations from the surface.

The cells forming the walls of the kidneys soon become large and vacuolated. This character is retained throughout the life of the animal, and makes the tracing of their cavities in some places a very difficult matter. Near the outer end of each kidney the cells are smaller, and the lumen is more easily traced. As the kidneys grow, they extend anteriorly and crowd dorsally beneath the pericardium and heart. As growth continues they become bent into loops, and numerous side pouches are formed.

Although much time has been spent in trying to find the inner, pericardial openings, of the kidneys, I have not succeeded in placing them. Cavities leading from the pericardium have frequently been traced nearly to the kidneys, but the vacuolated condition of the cells that compose their walls makes it very difficult to trace cavities with accuracy. I have no reason to suppose that the pericardial openings do not exist. I have simply been unable to find them.

In the adult, the ducts of the genital organs pass close to the lateral extremities of the pericardium. Near its end each duct turns toward the median line, meets the outer end of the kidney on the same side of the body, and opens with it into the mantle chamber. This connection is easy to demonstrate. Whether the genital ducts also communicate with the pericardium, or with the inner ends of the kidneys, I am not prepared to say.

GENITAL ORGANS.

The genital organs appear after the animal has become adult in most other respects. Each genital organ consists, at first, of a short and rather narrow tube that lies close to the pericardium, for the most part in contact with it. Whether this tube originates from the pericardium, or whether it is formed in some other way, has not been determined. The genital organs grow rapidly, and extend anteriorly and dorsally over and among the lobules of the liver, which are now very numerous. Soon the eggs and sperm begin to be formed, and the sexes can be distinguished. The eggs are few in number, but they are large and brown. The sperm are very numerous, of moderate size, and pale yellow. These colours are imparted to the genital organs. As their products begin to mature, the genital organs become very extensive and crowd between and around other organs, until all available space is filled.

The genital ducts of the adult, as in the young, connect with the outer ends of the kidneys, and with them open into the mantle chamber.

SUMMARY.

The young embryos of Nucula delphinodonta and Yoldia limatula resemble each other in most respects. They differ considerably in appearance, because of the difference in the size and distribution of the surface cilia. In the case of Yoldia the apical cilia are long and bunched together, and the cilia on the three intermediate rows of test-cells are collected into bands (text-fig. F). In Nucula delphinodonta all of the cilia on the surface of the embryo are short and evenly scattered (text-fig. E). The embryos of Yoldia swim freely in the water, and have to depend on their own activities for safety. The embryos of Nucula delphinodonta develop in a protecting brood-sac (fig. 1). It is to the advantage of these embryos to remain in the brood-sac, so active locomotion would not only be of no value, but it would be a positive danger. The possession of a test that is not functional as an organ of locomotion probably indicates that the embryos of the ancestors of Nucula delphinodonta were free-swimming. They then probably corresponded closely in appearance to the embryos of Yoldia limatula and Nucula proxima, both of which have the apical tuft and the bands of cilia.

The presence of a separate anal opening in the test, an extensive apical plate, and the formation of the cerebral ganglia without invaginations (fig. 24), are points in which Nucula delphinodonta differs from Yoldia. Nucula delphinodonta sheds its test when the foot is very immature.

The development of many of the organs of Yoldia has not been traced. The following is a brief review of the organs of Nucula delphinodonta.

Test.—The test consists of five rows of flattened cells, that together cover the greater portion of the body of the embryo. The cilia on the test are short and evenly distributed. The size and distribution of the cilia are probably the result of the protection afforded the developing embryo by the brood-sac. The test is finally thrown away. It is probably homologous to the velum of most Lamellibranch embryos. (See pp. 23-26, and figs. 11, 24, 25, 34, and 35.)

Apical Plate.—The apical plate is quite extensive, and bears short diffuse cilia that resemble the cilia on the test cells. The size of the apical cilia is probably also the result of the protection afforded the developing embryo by the brood-sac. The apical plate is thrown away with the test. (See pp. 26 and 27, and figs. 11 and 24.)

Shell.—The shell begins to form some time before the test is shed. The prodissoconch has a rounded outline and a short straight hinge-line. The adult shell is very robust. (See pp. 27 and 28, and figs. 20, 36, 50, and 51.)

Mantle.—The mantle lobes are formed by the growth and folding of the shell-gland. There are no tentacles on the margins of the mantle, and no siphons are formed. (See p. 29, and figs. 8, 17, 20, 48, and 69.)

Foot.—The foot is formed by the growth of tissue that, at first, lies between the stomodæum and the gut. At the time the test is shed it is very small and cannot be moved. The side flaps are developed as the result of unequal growth of the ventral side of the foot. The foot is a remarkably good burrowing organ, and it seems never to be used in creeping. (See pp. 30-33, and figs. 25, 28, 34, 36, 39, 40, 41, 48, 49, and 69.)

Byssal Gland.—The byssal gland is formed as an invagination on the ventral surface of the foot soon after the test is shed. It becomes very extensive, but in the adult is quite small. It seems never to form fibres. (See p. 33 and 34, and figs. 39, 40, 41, 45, and 48.)

Alimentary Canal.—The primitive gut is formed by the separation and division of cells on one side of the embryo. It is carried further into the interior by the addition of cells around the blastopore. These cells form the stomodæum. Later the gut grows posteriorly, beneath the shell-gland, and forms the stomach and intestine. The anus opens into the mantle chamber near the anal pore in the test. The future shape of the intestine seems to depend upon the position of certain organs during its elongation. (See pp. 34-39, and figs. 8, 9, 11, 15, 24, 25, 34, 36, 40, 45, 46, 47, and 48, and text-figs. M to S.)

Labial Palps.—The labial palps are marked out as patches of cilia about the time that the third lobe of the gill begins to form (fig. 41). The ciliated patches along the sides of the body are bent so as to form grooves (fig. 62, *lp.*) ; the dorsal portions of the patches form the outer palps, and the ventral portions the inner palps. The palp appendages are formed by unequal growth of the posterior portion of the outer palps, and each corresponds morphologically to a pair of ridges with a groove between them. They can be extended beyond the margins of the shell, and they are used as food collectors. (See pp. 39-43, and figs. 41, 45, 47, 48, 54, 55, 56, 57, 58, 59, 60, 62, and 66.)

Gills.—The gills are formed as folds on the inner sides of the lobes of the mantle. The folds form lobes that grow to form filaments and finally plates. The inner plates are formed first. The outer plates are formed by growth at the bases of the inner plates. A study of their development throws no light on the phylogeny of the gills. (See pp. 43-49, and figs. 39, 40, 41, 45, 48, 52, and 53.)

Hypobranchial Glands.—The hypobranchial glands are formed about the time that the animals become sexually mature. They seem to furnish the secretions from which the brood-sac is formed, and they may have other functions. (See pp. 49 and 50.)

Pericardium.—The pericardium is a remnant of a cavity that probable represents a schizocœle. Its epithelial lining seems to be formed by the rearrangement of mesodermal cells. (See pp. 50-52, and figs. 24, 26, 28, 34, 35, 36, 39, 41, and 48.)

Vascular System.—The heart is formed as a mesodermal strand that stretches across the pericardium from one side to the other. There is no indication that it is formed by the fusion of either a pair of pouches or two masses of cells. It seems to be single in its origin. It is formed around the intestine, but later becomes free and dorsal to it. This seems to show that for this group, at least, the dorsal position of the heart as found in the adult is not primitive. The vascular system consists largely of spaces that occur in all parts of the body. (See pp. 52-55 and figs. 41, 48, 67, 68, and 69.)

Nervous System.—The cerebral and pedal ganglia are about equal in size, and the visceral ganglia are considerably smaller. The cerebro-visceral commissures are very large, and contain many scattered nuclei. The cerebro-pedal commissures show ordinary structure. It is suggested that the smaller, dorsal roots of the cerebro-pedal commissures may be the central ends of the otocystic nerves. (See pp. 55-59, and figs. 24, 34, 36, 40, 46, and 48.)

Otocysts.—The otocysts are formed as invaginations from the body-wall soon after the test is shed. They seem to be entirely closed off, but canals connecting them with the surface are present in the adult. The otoliths are irregular bodies, but they are probably formed in the otocysts themselves. (See pp. 59-61. and figs. 40, 46, 48, and 64, and text-fig. W.)

377, and figs. 40, 46, 48, and 64, and text-fig. W.)

Muscular System.—The muscular system is well developed, and resembles the muscular system of Yoldia in most respects. The extensive attachments of the foot muscles to the dorsal portion of the shell is accounted for by the great development of these muscles. (See pp. 61-64.)

Excretory Organs.—The vacuolated character of the cells of the execretory organs makes it difficult to trace some portions of the cavities of these organs. The inner, pericardial openings, are hard to find. The outer end of each excretory organ opens into the mantle chamber, in connection with the genital duct of the same side. (See pp. 64 and 65.)

Genital Organs.—The genital organs are formed after the animal is adult in most other respects. They can first be distinguished as short tubes that lie very close to, or in contact with, the pericardium, and open into the mantle chamber in connection with the outer ends of the kidneys. The genital organs become very extensive in the adult. The sexes are separate. (See p. 65.)

Most of the work necessary for the preparation of this paper was done in the Biological Laboratory of the Johns Hopkins University. To many that are now or formerly were connected with that laboratory, and especially to Professor W. K. Brooks, I am indebted for suggestions and encouragement. I also desire to express my appreciation of the courtesies extended to me by Professor C. O. Whitman, at the Marine Biological Laboratory. I am particularly indebted to my wife, who has, among other things, performed a great share of the work connected with the care and preservation of material. Beside the work at the seashore, embryos obtained in June were kept alive in Baltimore from October 1st until January 1st, with water sent from the sea.

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EXPLANATION OF PLATES

Reference Letters

aa. Anterior adductor muscle. *aas.* Anterior adductor muscle-scar. *ap.* Apical plate. *bg.* Byssal gland. *bs.* Blood-space. *ca.* Cartilage. *cg.* Cerebral ganglion. *cp.* Cartilage pit. *cs.* Chitinous support. *ec.* Ectoderm. *f.* Foot. *g.* Gill. *gs.* Suspensory membrane of gill. *h.* Heart. *int.* Intestine. *ip.* Inner plate of the gill. *ilp.* Inner labial palp. *k.* Kidney. *l.* Liver. *lm.* Longitudinal muscle. *lp.* Labial palp. *m.* Mantle. *mg.* Mid-gut. *mo.* Mouth. *oes.* Œsophagus. *olp.* Outer labial palp. *op.* Outer plate of the gill. *ot.* Otocyst. *pa.* Posterior adductor muscle. *pap.* Palp appendage. *pas.* Posterior adductor muscle-scar. *pg.* Pedal ganglion. *pn.* Palp nerve. *sg.* Shell-gland. *std.* Stomodæum. *sto.* Stomach. *t.* Test. *tc.* Cavities in the mantle caused by teeth on the shell. *v.* An organ of unknown function. *vg.* Visceral ganglion. *y.* Cut wall of gill plate. *z.* Scattered cells of the disorganised liver.

PLATE 20.

Fig. 1.—Adult specimen with the brood-sac attached. The brood-sac is torn open to show the eggs inside. × 10.

Fig. 2.—Sixteen-celled stage. × 150.

Fig. 3.—Section of an embryo in the sixteen-celled stage. × 275.

Fig. 4.—Section of a later cleavage stage that corresponds to an epibolic gastrula. The asterisk (*) marks the position where the gut is formed. × 275.

Fig. 5.—An embryo that is slightly older than the one represented in section by Fig. 4. × 150.

Fig. 6.—Lateral view of an embryo in which the gut has been formed, represented as a slightly transparent object. From the study of preserved material I am inclined to think that the shell-gland does not bear cilia, but this has not been determined on living material. The line marked 7 indicates the plane in which the section, Fig. 7, was taken. × 150.

Fig. 7.—Transverse section of an embryo in the stage represented by Fig. 6. The line 7, on Fig. 6, indicates the plane of the section. × 275.

Fig. 8.—Sagittal section of an embryo in the stage represented by Fig. 6. × 275.

Fig. 0.—Sagittal section of an embryo slightly older than the embryo of which Fig. 8 is a section. It represents the beginning of the formation of the stomodæum. × 275.

Fig. 10.—Dorsal view of an embryo in which the test is growing over the shell-gland. The lines numbered 11, 12, and 13 indicate the planes of sections represented in corresponding figures. × 150.

FIG. 11.—Sagittal section of an embryo in the stage represented by Fig. 10. The line 11 on Fig. 10 indicates the plane of the section. × 275.

FIGS. 12 and 13.—Transverse sections of an embryo in the stage represented by Fig. 10. The lines 12 and 13 on Fig. 10 indicates the planes of the sections. × 275.

PLATE 21.

FIG. 14.—Lateral view of an embryo in which the test is fully formed, represented as a slightly transparent object. The lines numbered 16, 17, 18, and 19 indicate the planes of sections represented in corresponding figures. × 150.

FIG. 15.—Sagittal section of an embryo in the stage represented by Fig. 14. The anterior ends point in opposite directions in the two figures. × 275.

FIGS. 16, 17, 18, and 19.—Transverse sections of an embryo in the stage represented by Fig. 14. The lines 16, 17, 18, and 19 on Fig. 14 indicate the planes of the sections represented by these figures. × 275.

FIGS. 20, 21, and 22.—Transverse sections of an embryo older than the one represented by Fig. 14, and a little younger than the embryo represented by Fig. 23. The lines 20, 21, and 22 on Fig. 23 represent planes that correspond to these sections. × 275.

FIG. 23.—Lateral view of an embryo in which the mantle is beginning to form, represented as a slightly transparent object. The lines 20, 21, and 22 indicate the planes of sections represented in corresponding figures, but the embryo represented in Fig. 23 is slightly older than the one from which these sections were obtained. × 150.

FIG. 24.—Sagittal section of an embryo in the stage represented by Fig. 23. × 275.

FIG. 25.—Lateral view of an embryo that would soon shed its test. The test cells, indicated in outline, are very indistinct, and are not accurately drawn. Cilia have been indicated along the margins only. They cover the whole of the surface. The organs are more clearly shown than in preceding figures of embryos. They are not visible in whole mounts, but have been reconstructed from sections. The lines 27, 28, 29, 30, 31, 32, and 33 indicate the planes of sections represented by these figures. (See Plate 22.) × 150.

PLATE 22.

FIG. 26.—Sagittal section of an embryo in the stage represented by Fig. 25, Pl. 21. × 275.

FIGS. 27, 28, and 29.—Transverse section of an embryo in the stage represented by Fig. 25, Pl. 21. The lines numbered 27, 28, and 29 on Fig. 25 indicate the planes of sections represented by these figures. × 275.

FIGS. 30, 31, 32, and 33.—Horizontal sections of an embryo in the stage represented by Fig. 25, Pl. 21. The lines numbered 30, 31, 32, and 33 on Fig. 25 indicate the planes of the sections represented by these figures. × 275.

PLATE 23.

FIG. 34.—Lateral view of a reconstruction of an embryo that has just completed the first step in the process of casting. The test cells, apical plate, and stomodæum still adhere to the anterior end of the embryo. × 150.

FIG. 35.—Lateral view of a reconstruction of an embryo that has completed the process of casting. × 150.

FIG. 36.—Lateral view of a reconstruction of an embryo in which the liver pouches have begun to go to pieces. × 150.

FIG. 37.—Sagittal section of an embryo in the stage represented by Fig. 36. × 275.

FIG. 38.—Transverse section of an embryo in the stage represented by Fig. 36, taken through the stomach just posterior to the pedal ganglia. × 275.

FIG. 39.—Lateral view of a reconstruction of an embryo that is just beginning to form the gills. × 150.

FIG. 40.—Lateral view of a reconstruction of an embryo in which each gill is beginning to form two lobes. × 150.

FIG. 41.—Lateral view of a reconstruction of an embryo in which each gill is beginning to form its third lobe. × 150.

FIG. 42.—Horizontal section of an embryo in a stage represented by Fig. 40, taken through the dorsal end of the stomach and the re-forming lobes of the liver. × 200.

FIG. 43.—Horizontal section of an embryo in the stage represented by Fig. 41, taken through the dorsal end of the stomach and the re-forming lobes of the liver. × 200.

FIG. 44.—Horizontal section of an embryo in the stage represented by Fig. 46, Pl. 24, taken through the dorsal end of the stomach and the re-formed lobes of the liver. × 150.

PLATE 24.

FIG. 45.—Lateral view of a reconstruction of an embryo in which each gill has four pairs of plates. × 125.

FIG. 46.—Lateral view of a reconstruction of an embryo in which each gill has six pairs of plates. × 125.

FIG. 47.—Lateral view of a reconstruction of an embryo in which each gill has eight pairs of plates. × 110.

FIG. 48.—Lateral view of a reconstruction of an adult specimen. × 30.

FIG. 49.—Adult specimen with the foot protruded and the side flaps spread apart. × 10.

FIG. 50.—View of the inside of an adult left shell-valve. × 15.

FIG. 51.—Left shell-valve seen obliquely from the dorsal margin. × 15.

FIG. 52.—A nearly horizontal section of an embryo in the stage represented by Fig. 46, cut to show the developing outer plates of the gills. × 150.

FIG. 53.—A pair of adult gill plates. The suspensory membrane, the continuous chitinous trough, the longitudinal muscle, and the walls of the plates that join the plates next in succession have all been cut across in removing the plates from the gill. (Drawn from a study of sections.) × 250.

PLATE 25.

FIGS. 54, 55, and 56.—Stages in the development of the labial palps. The palps have been carefully drawn, but for the sake of clearness they have in each case been represented with the outer palp on the right side turned away from the corresponding inner palp. The foot is represented as cut off, and the specimen is turned so that the mouth can be seen between the palps. × 125.

FIG. 57.—The posterior portions of the right outer and inner palps of an adult specimen. The two palps are represented as spread apart and placed in a position that corresponds with Fig. 56. × 65.

FIGS. 58, 59, and 60.—Successive sections of the labial palps of a specimen that has six pairs of gill plates. The sections are taken transverse to the embryo. The stage is much the same as is represented by Fig. 54. Fig. 58 is near the mouth, Fig. 59 is near the posterior end of the outer palp, and Fig. 60 is posterior to the outer palp. × 150.

FIG. 61.—Transverse section of an embryo with four pairs of gill plates (see Fig. 45, Plate 24) taken through the mouth. × 200.

FIG. 62.—Transverse section of an embryo with four pairs of gill plates, taken just anterior to the stomach. × 200.

FIG. 63.—Sagittal section of the antero-dorsal portion of an embryo that has eight pairs of gill plates. × 150.

FIG. 64.—Horizontal section of the foot of an embryo that has six pairs of gill plates, taken just ventral to the mouth. × 150.

FIG. 65.—Horizontal section of the foot of an embryo that has six pairs of gill plates, taken through the mouth. × 150.

FIG. 66.—Transverse section of the palp appendage of an adult specimen. × 200.

FIG. 67.—A nearly transverse section of an embryo that has five pairs of gill plates, taken through the heart. × 200.

FIG. 68.—A diagonal section of an embryo that has nine pairs of gill plates, taken through the heart. × 90.

FIG. 69.—A diagonal section of an adult specimen, taken through the heart. × 45.

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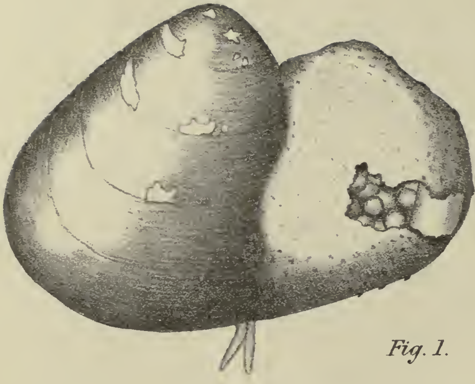

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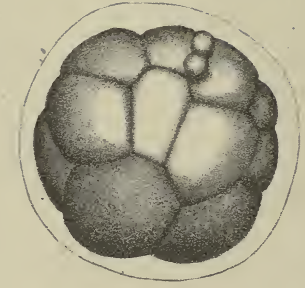

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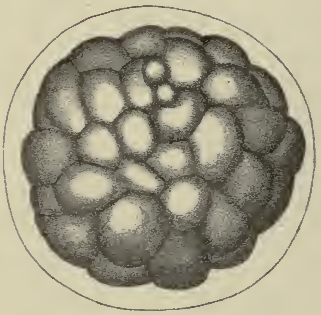

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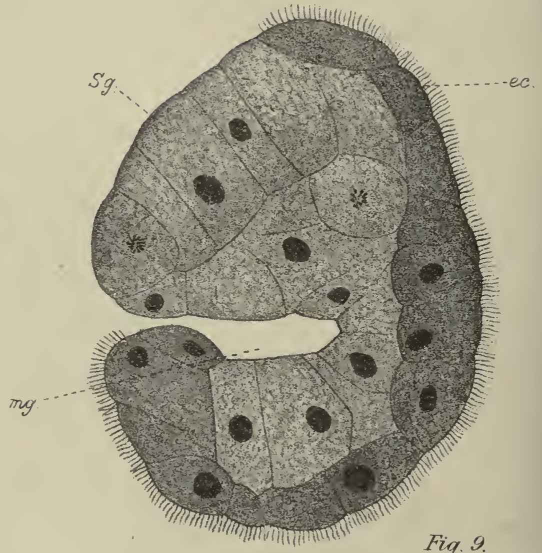

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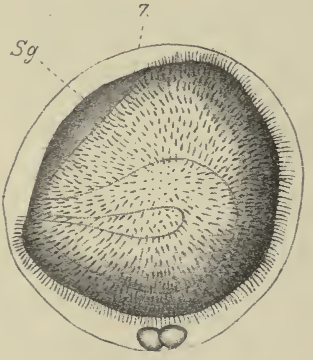

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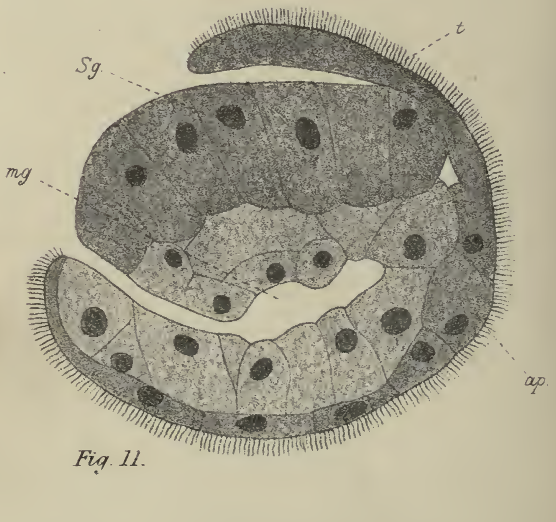

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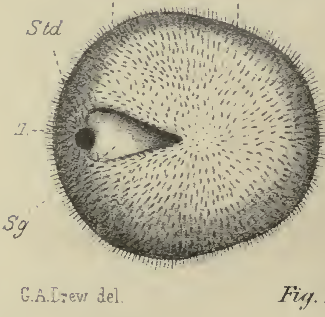

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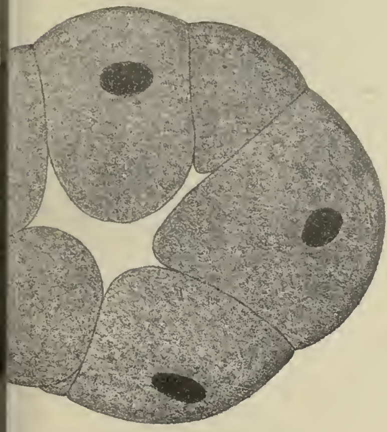

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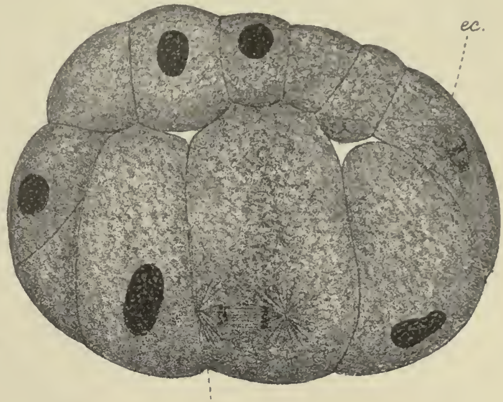

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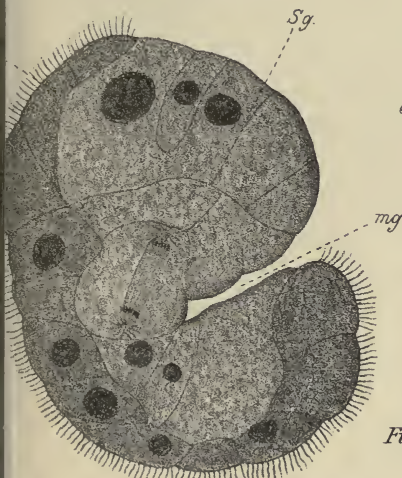

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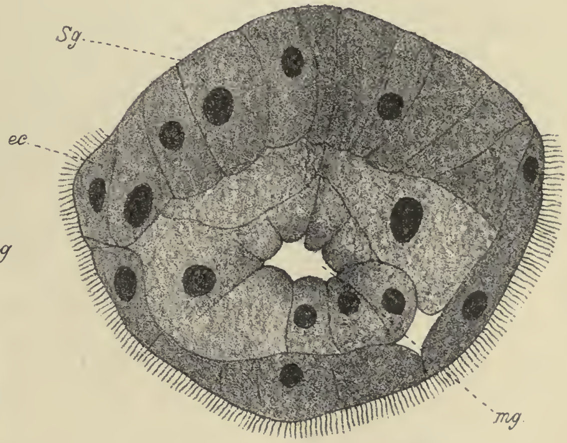

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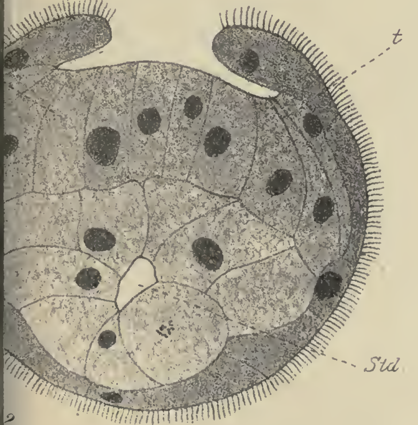

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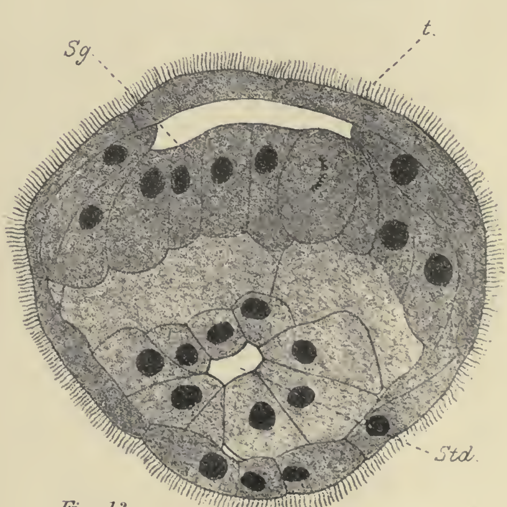

Fig. 13.

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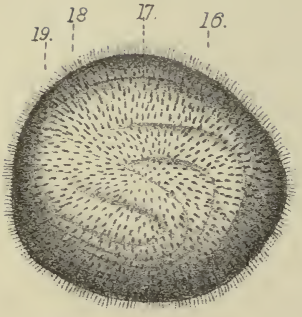
Fig. 14.



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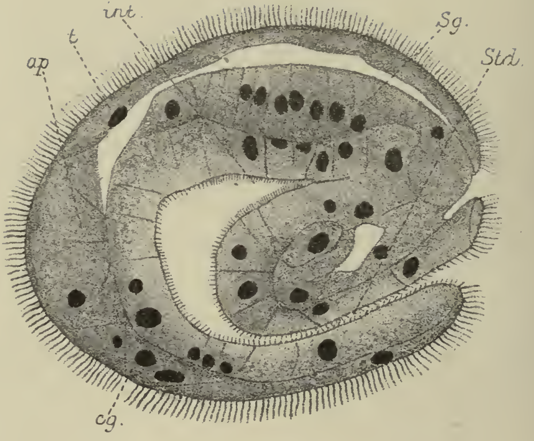

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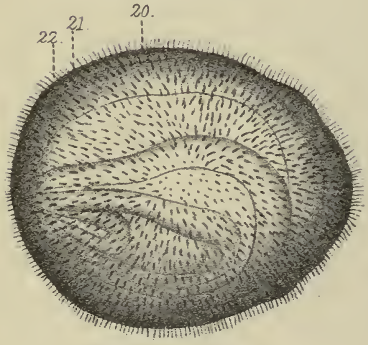

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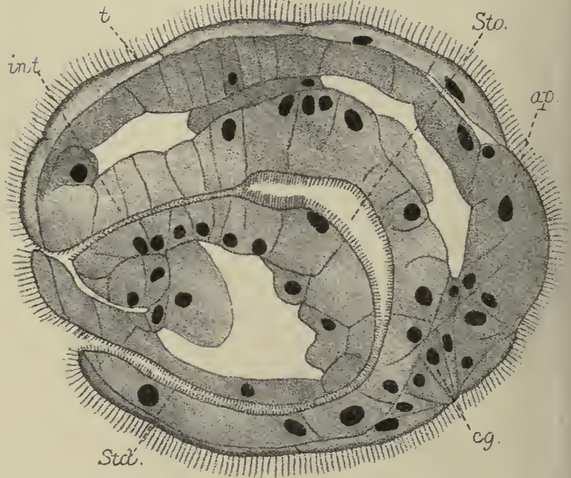

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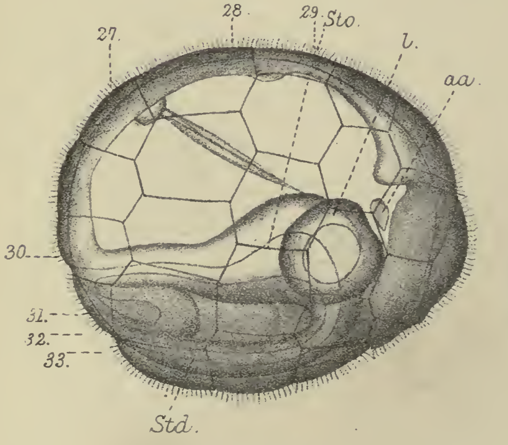

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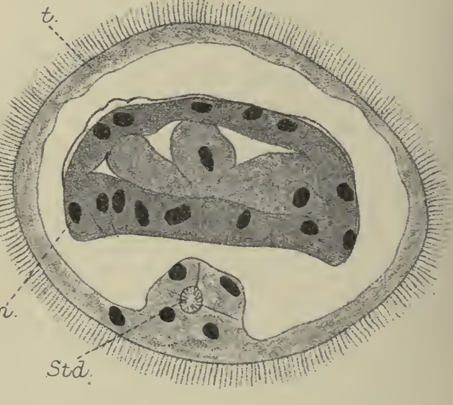

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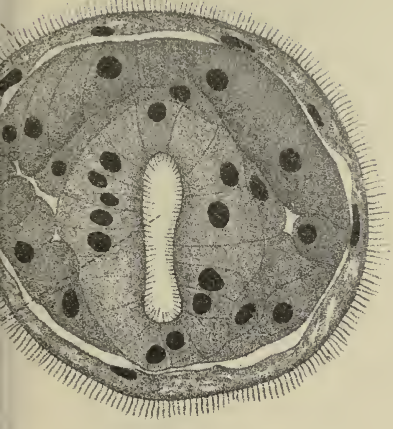

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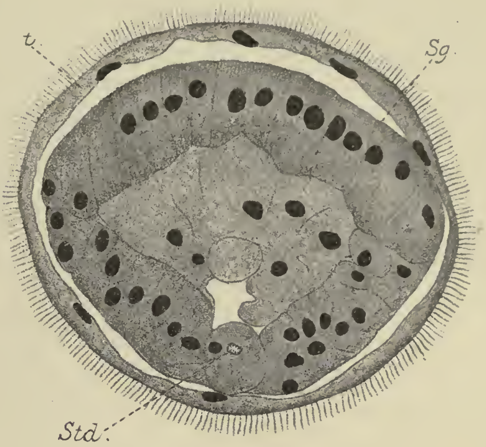

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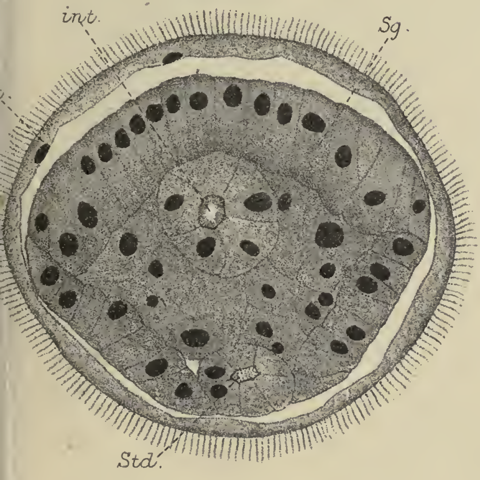

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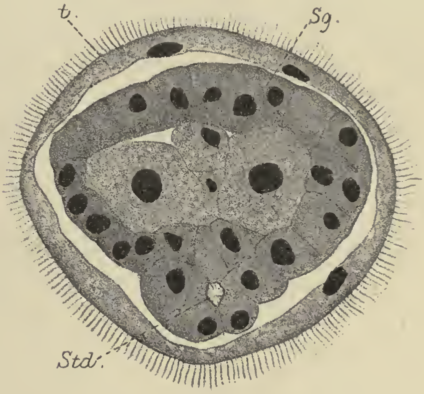

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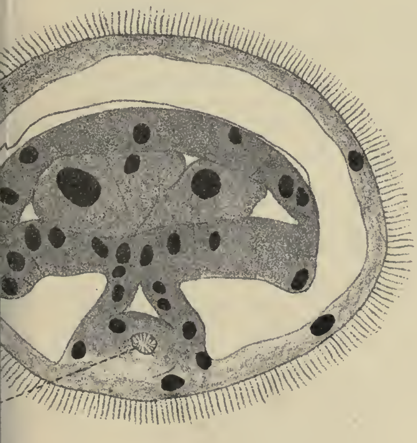

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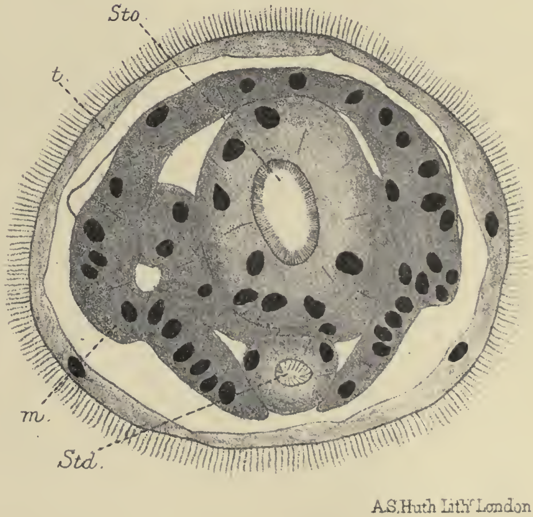

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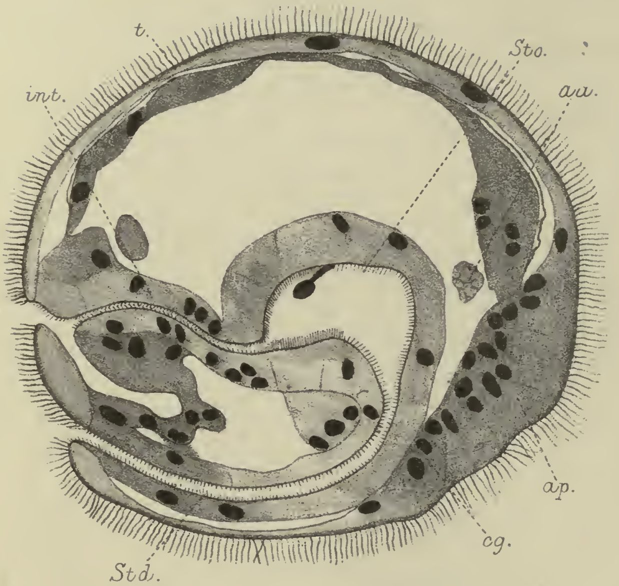

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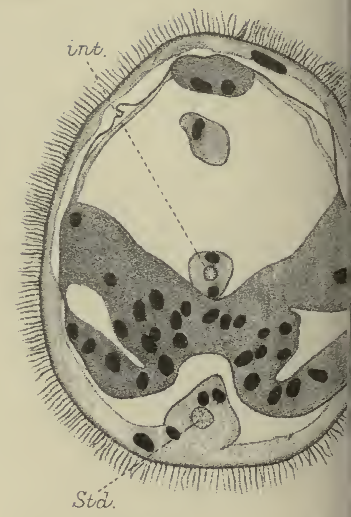
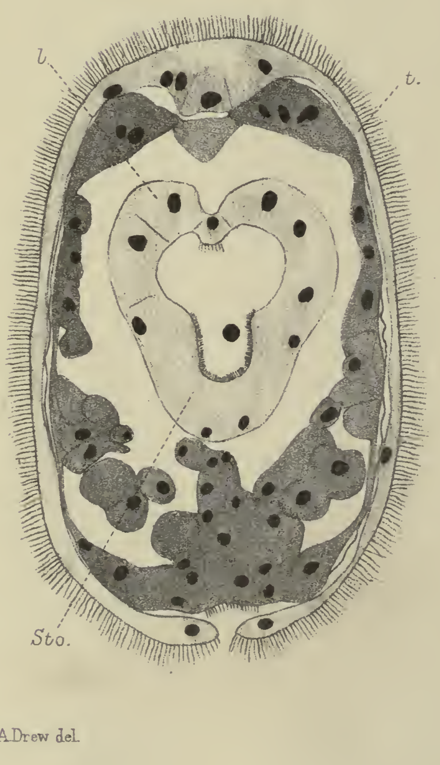


Fig. 30.



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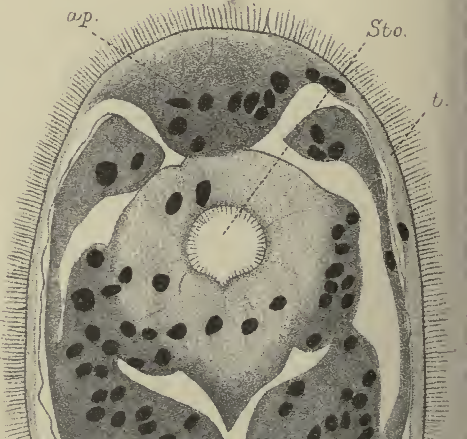

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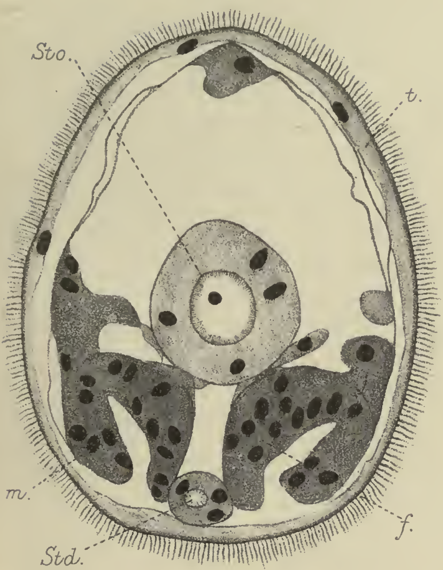

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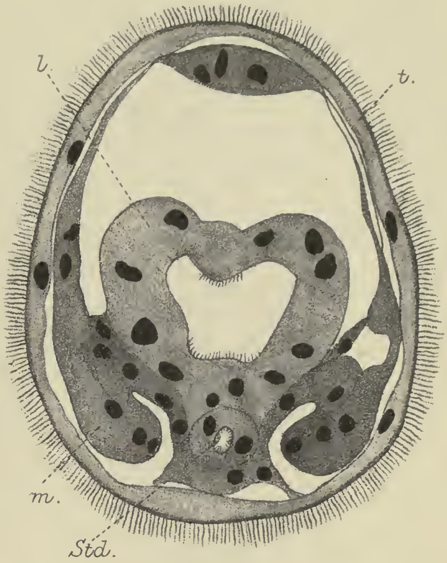

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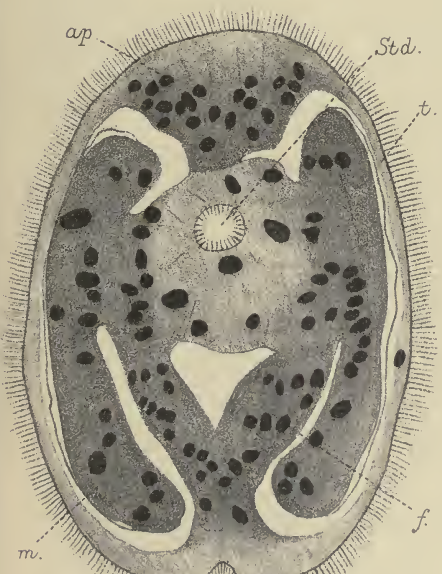

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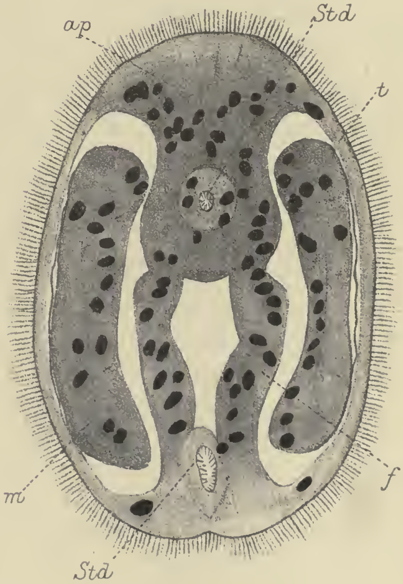

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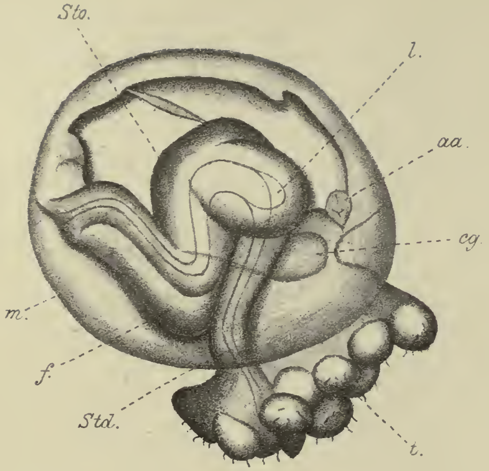

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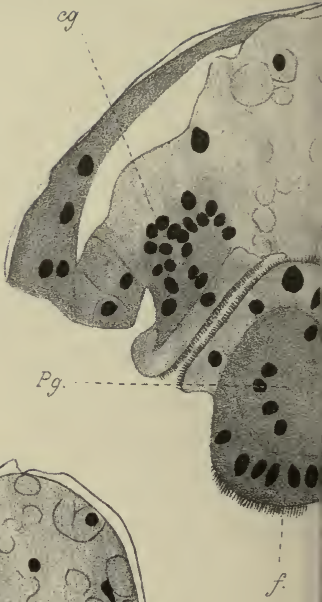

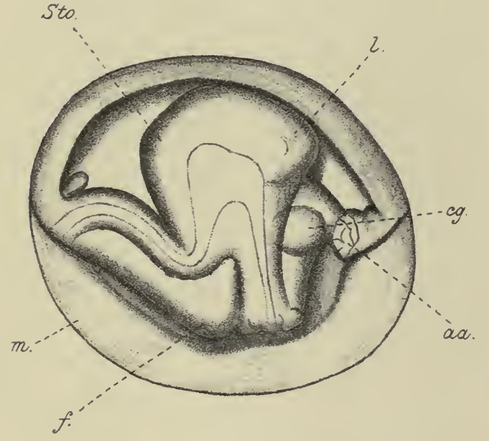

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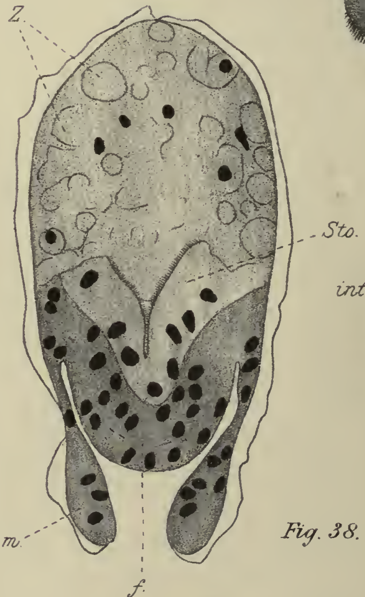

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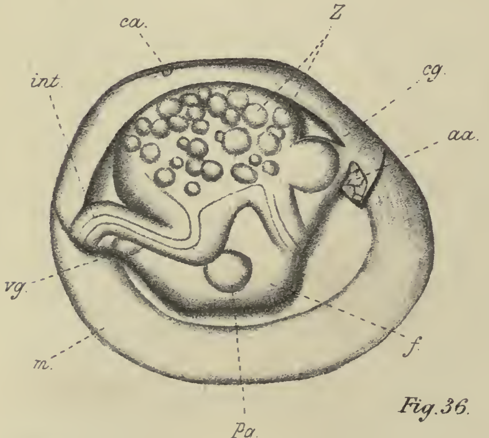

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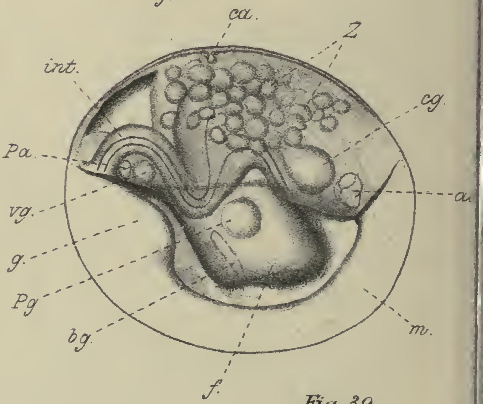

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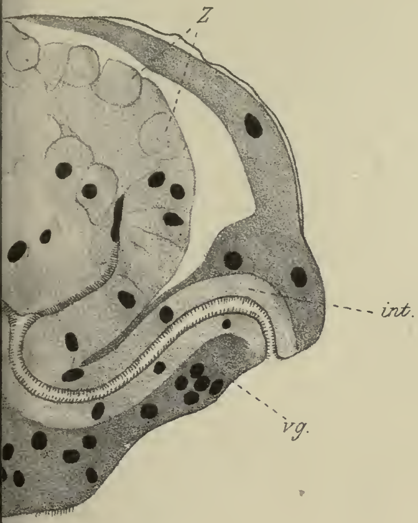

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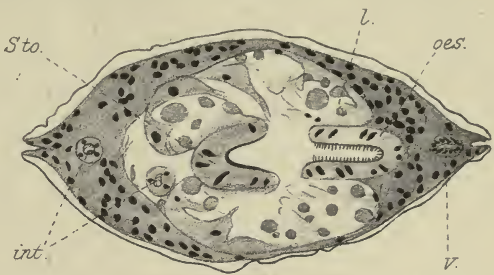

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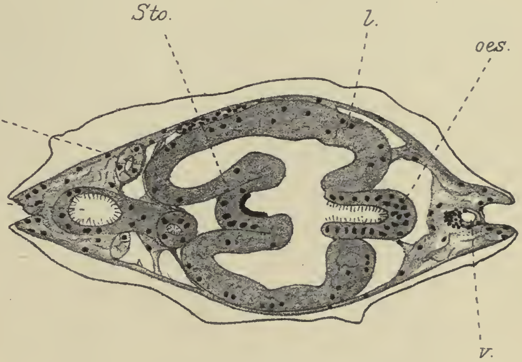

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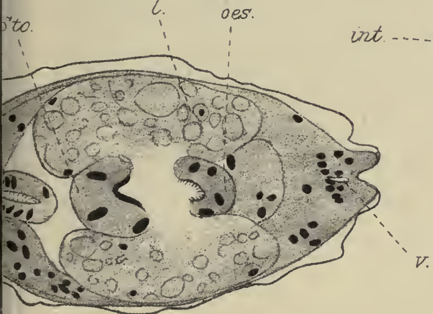

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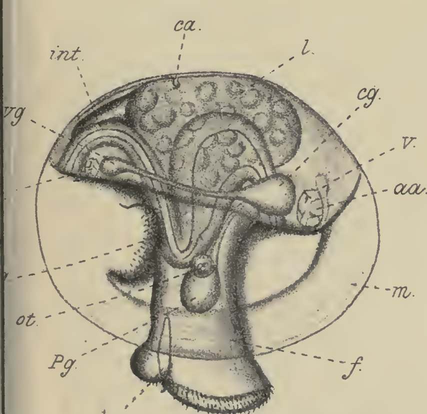

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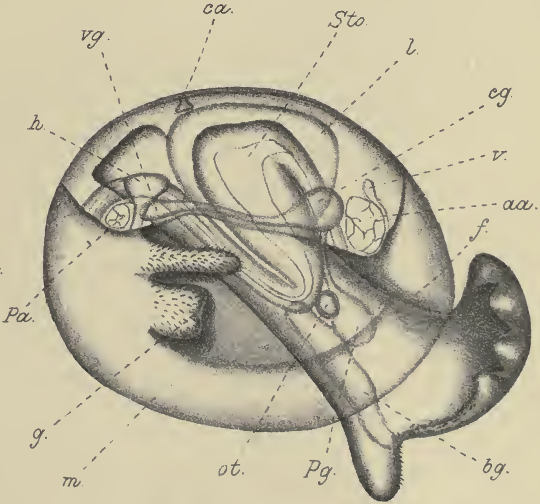

Fig. 41.

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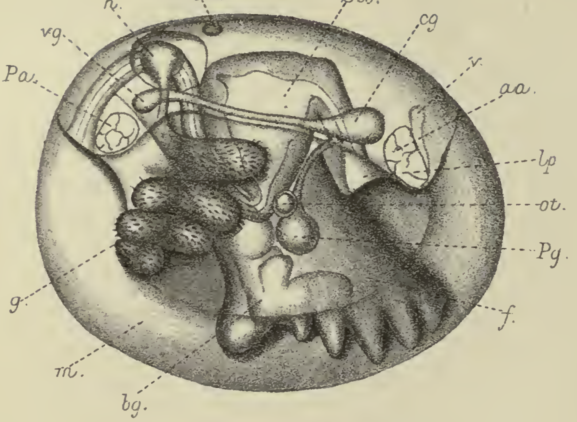

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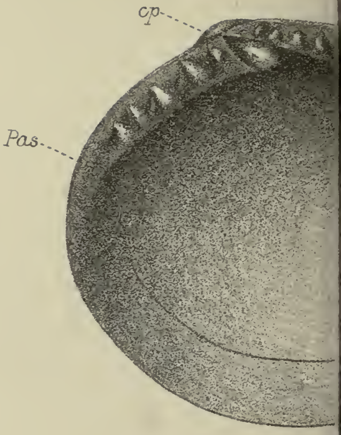

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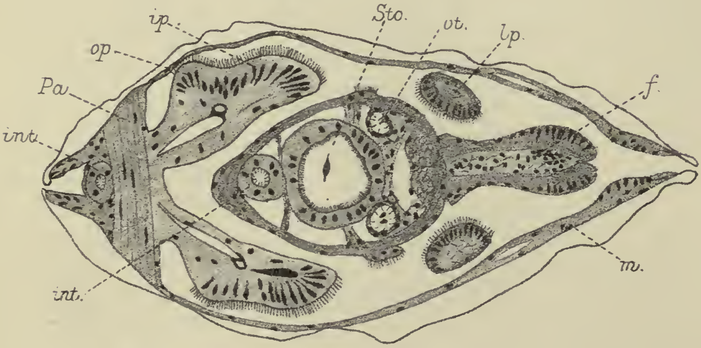

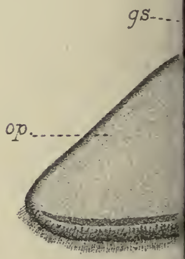

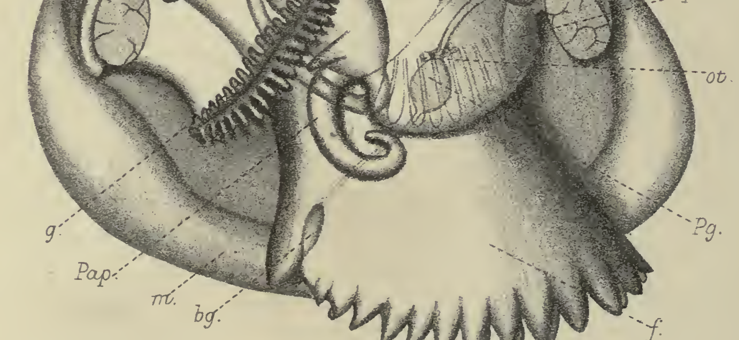

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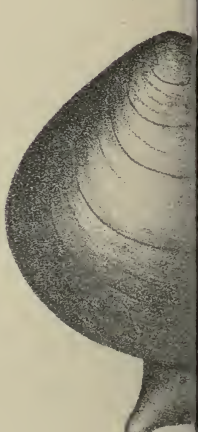

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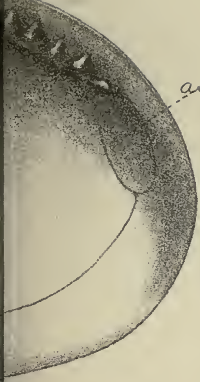

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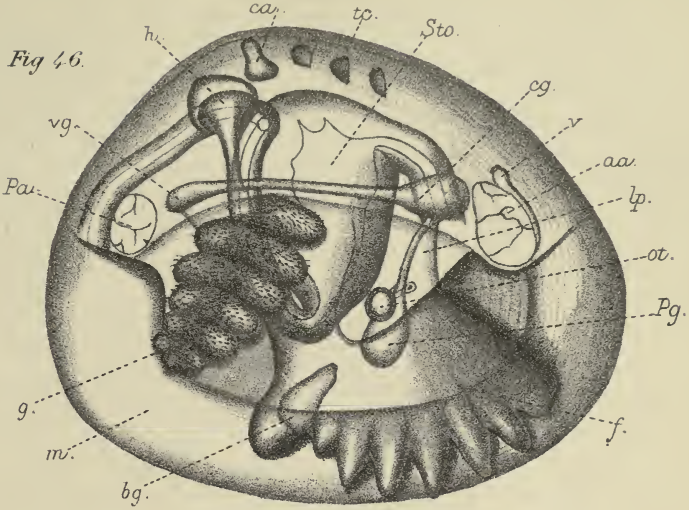

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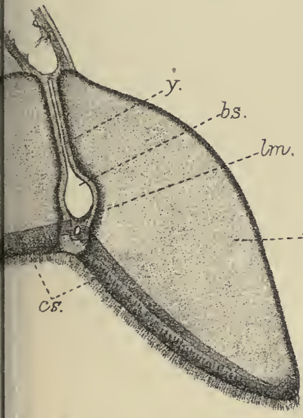

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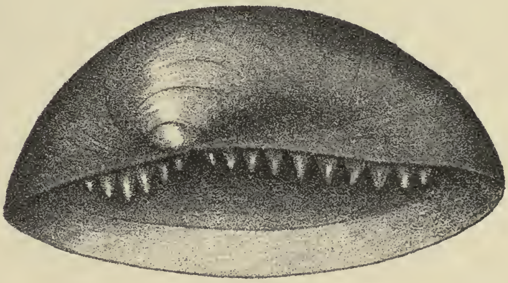

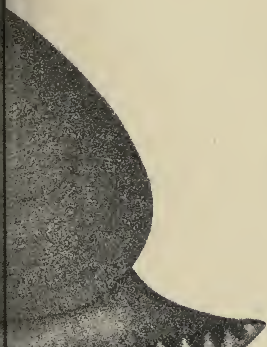

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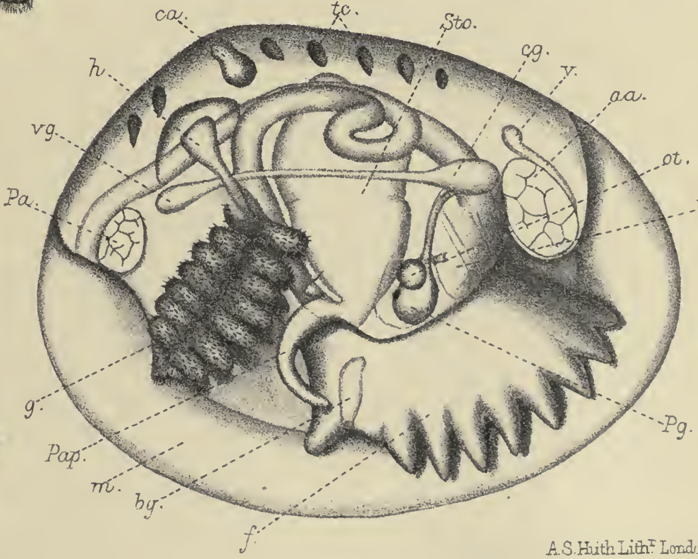

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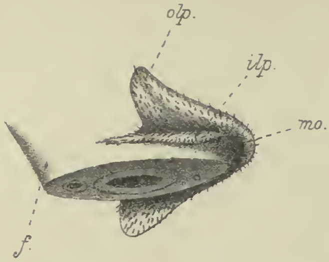

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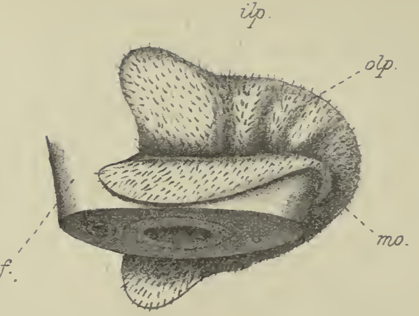

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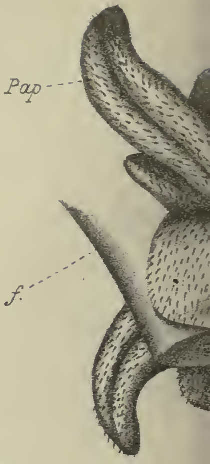

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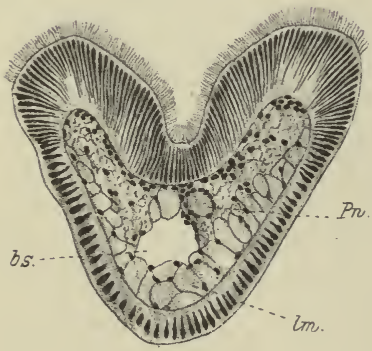

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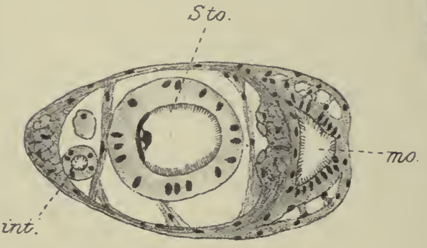

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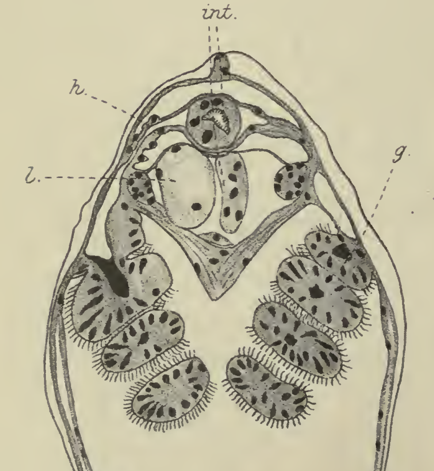

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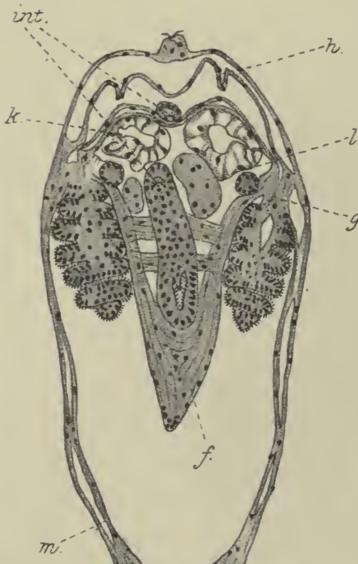

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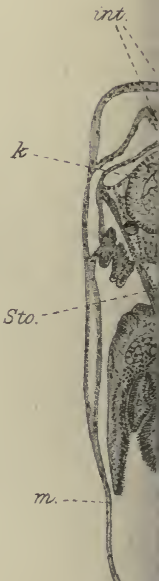

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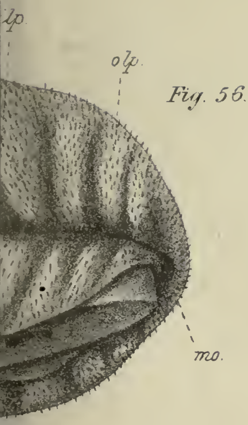

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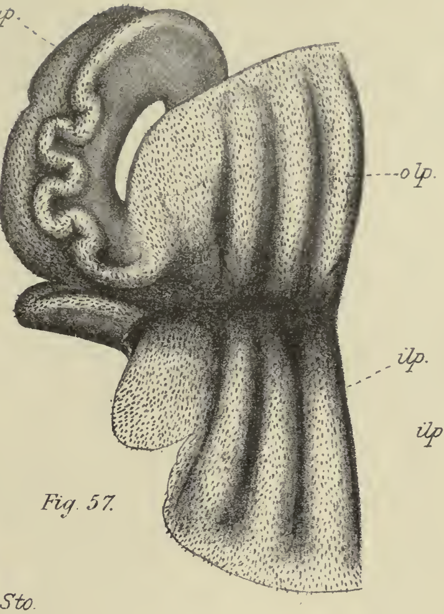

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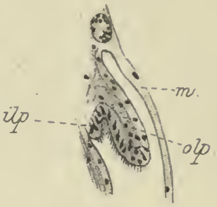

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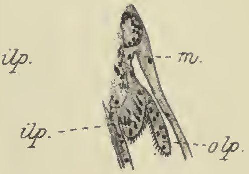

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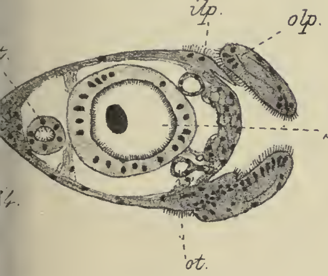

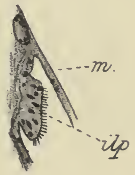

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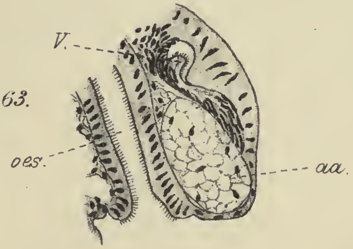

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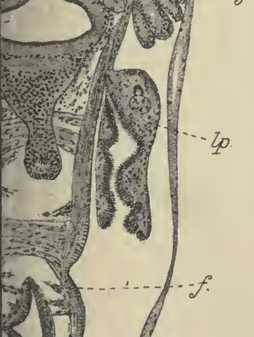

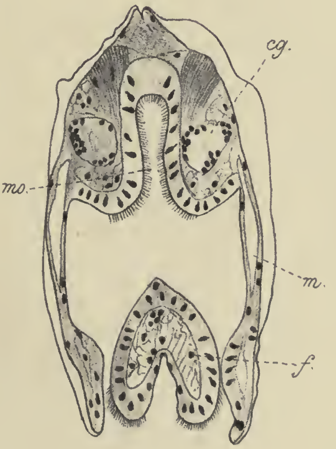

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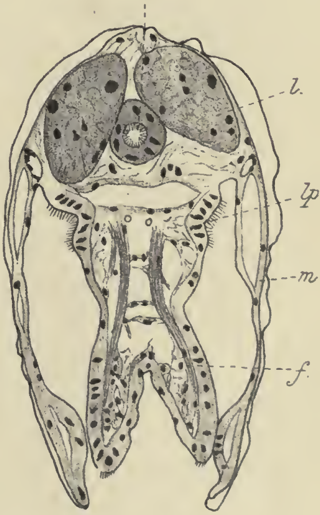

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